INVESTIGATIONS INTO STICKLEBACK SOCIAL LEARNING
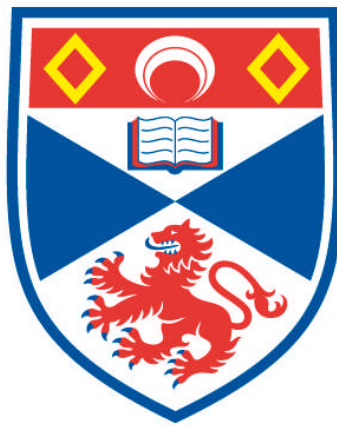
Nicola Atton

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

2014

**Full metadata for this item is available in
Research@StAndrews:FullText
at:
http://research-repository.st-andrews.ac.uk/**

**Please use this identifier to cite or link to this item:
http://hdl.handle.net/10023/6610**

Investigations into Stickleback Social Learning

Nicola Atton

Thesis submitted to the School of Biology of the University of St. Andrews for the degree of Doctor of Philosophy

October 2013

Acknowledgements

I would like to acknowledge a number of people who have helped make this thesis possible. Mike Webster in particular has played an integral part. He helped me design and setup all experiments presented here. He spent many hours with me catching sticklebacks in the Kinnesburn, often in truly despicable weather. He has also provided very helpful advice with regards to data analysis and proof read every chapter.

Will Hoppitt has also been of great assistance. He designed and implemented the version of NBDA used in chapters 6 and 7 and was a great help in writing the methods and results sections of those chapters with regards to the data analysis.

My two supervisors, Kevin Laland and Jeff Galef, have provided valuable insight and advice for this thesis in its entirety.

I would also like to thank my friends and colleagues in the Laland lab, in particular Laurel Fogarty, Alice Cowie, Tom Morgan, and Lewis Dean for providing the necessary commiseration and camaraderie when experiments inevitably 'went wrong'.

Finally I would like to thank my husband Drew for all his support over the years. Without his persistent nagging, I likely never would have gotten it finished.

Abstract

The objective of the experiments contained within this thesis was to provide further insight into the social learning capabilities of threespined sticklebacks and the factors affecting the transmission of information through populations.

There are a number of previous studies which provide evidence that both threespined and ninespined sticklebacks possess the ability to learn socially under a range of contexts, such as foraging, anti-predator behaviour, mate choice, and cooperation. The studies presented in this thesis aim to extend this knowledge and shed light on the social learning processes used.

Evidence was found to support previous opinion that threespined sticklebacks are capable of using a number of social learning processes, including local enhancement, stimulus enhancement, and the social enhancement of food preferences. However, there was no evidence to suggest that either threespined or ninespined sticklebacks are capable of using the social learning process of delayed local enhancement under a shelter choice context, a process which both species have previously been shown to use under a foraging context.

This thesis also explores the effect of the social network within shoals of threespined sticklebacks upon the transmission of novel foraging information. It was discovered that both prior association preferences and prior diet have an effect on the order in which individuals discover a novel foraging task.

Contents

Chapter 1. An Introduction to Animal Social Learning

In this chapter I shall introduce the reader to the concept and previous literature surrounding the topic of animal social learning. I shall start by discussing the different forms of learning and use these to help understand the process of social learning. I shall then outline the different social learning processes that have been identified and give examples of each. I will also present empirical evidence for the different social learning strategies that exist and end with a review of the literature regarding the different contexts under which social learning has been identified, specifically in fish.

1.1 The importance of social learning

In a dynamic environment, information about biologically important aspects of life, such as the location of the most profitable food patches, the most nutrient rich food types, areas safe from predators, and the best mates, rapidly becomes outdated. Animals are therefore required to gather information about their environment in order to make biologically important decisions that can increase their fitness and chances of survival. The way they gather this information can vary. They can either choose to collect it for themselves by exploring and interacting with their immediate surroundings (asocial learning) or they can learn this information from others (social learning). Much of the relevant information required to make these decisions must be collected and learned rapidly if an individual is to avoid mishap. For example, a fledgling bird must learn to avoid predators before it is predated upon, or learn to select food items of the most nutritional value before internal reserves are exhausted (Galef and Laland 2005). Juveniles (and other naive individuals) of many species therefore benefit greatly from interactions with adults and other well informed individuals that have already acquired

successful patterns of behaviour allowing them to thrive in their environment by avoiding predators, consuming a nutritious diet, and know the locales of water and safe refuges (Galef and Laland 2005). In using the behaviour of informed individuals to guide the development of their own behavioural repertoires, juveniles and other naive individuals are consequently able to acquire the optimal behavioural responses to the demands of the particular environment in which they are residing without incurring many of the costs associated with individual trial-and-error learning (Galef and Laland 2005).

Both asocial and social learning are types of phenotypic plasticity allowing individuals to acquire behaviour that is adaptive within their local environment (Boyd and Richerson 1988). However, theory has shown that when the environment is dynamic (as is the case in most, if not all, habitats), social learning proves to be the more advantageous. Rendell et al. (2010) organised a computer tournament in which multiple strategies where entered specifying how to use social learning and asocial learning to acquire adaptive b*e*haviour in a complex environment. Strategies that relied predominantly on social learning were found to be the most successful, even when asocial information was no more costly to acquire than social information (Rendell et al. 2010).

1.2 What is animal social learning?

1.2.1 Learning theory

Before we can begin to understand and define animal social learning and how it manifests, we must first address the more general issue of animal learning as a whole, whether it be through social or asocial means. The most widely accepted definition of

animal learning within contemporary animal learning theory is "a change in an animal at a certain time, t_1 that is detectable later, t_2, in that animal's behaviour" (Rescorla 1988, Heyes 1994). Here I give a brief introduction to animal learning theory in its two most basic forms; associative learning and single-stimulus learning.

1.2.1.1 Associative learning

An important milestone in the theory of associative learning in animals was proposed by Edward Thorndike in 1898, who regarded learning as a direct result of connections being formed between stimuli and responses. Thorndike's theory was based on what has since been coined 'instrumental' or 'operant conditioning', whereby the probability of an individual performing a behaviour (R) either increases or decreases in response to an environmental stimulus (S) depending on whether S is appetitive or aversive respectively. For example, exerting pressure on a lever (R) may either result in a positive stimulus such as a food reward, or a negative stimulus such as an electric shock (S). The former will result in an increase in the probability of performing behaviour R and the latter will result in a decrease in the probability of performing behaviour R.

A second form of associative learning is 'classical' or 'Pavlovian conditioning'. In this form of learning it is not an individual's behaviour that is coupled with a positive or negative stimulus (unconditioned stimulus, US), but rather a second, neutral stimulus (conditioned stumulus, CS), with the animal forming an association between the two events. For example, Pavlov's dogs would salivate upon hearing a bell (CS) after the sound had previously been repeatedly paired with the presentation of food (US).

1.2.1.2 Single-stimulus learning

Single-stimulus learning is a non-associative learning mechanism where repeated exposure to a single stimulus (an object or event in an animal's environment) elicits a change in an animal's behaviour. This behavioural change could either result in the animal being more likely to respond to the stimulus (sensitisation) or less likely to respond (habituation).

1.2.2   Social learning definitions and processes

Social learning is essentially the acquisition and utilisation of information produced by others, or can be more specifically defined as "learning that is facilitated by observation of, or interaction with, another individual (or its products)" (Hoppitt and Laland, 2013).This relatively broad definition has been further refined with the identification of many different mechanisms by which such learning can occur; social learning processes. Typically, individuals that acquire and or utilise information gathered via social means are described as 'observers', whilst those that provide the information are labelled as 'demonstrators'. Below I give a brief review of each of the social learning processes that have been identified and outline the patterns of behaviour of the observers and demonstrators found in each.

1.1.2.1. Imitation

Imitation was first described by Thorndike (1898, pg. 50) as "learning to do an act by seeing it done". This definition has since been refined several times within the social learning literature, however, consensus on the exact definition and the criteria required for imitation has yet to be reached. For example, whether or not there is evidence of intentional copying, how accurately the observer must copy the demonstrator, and

whether or not the behaviours copied must be novel to the observer are bones of contention (see Hoppitt and Laland 2008 for a more detailed discussion).

With regards to the latter point of novelty the process of imitation can be divided into two sub-categories, contextual imitation and production imitation. Contextual imitation can be said to have occurred when "directly through observing a demonstrator perform an action in a specific context, an observer becomes more likely to perform that action in the same context." (Hoppitt and Laland 2008, p.117). Hence what is acquired is knowledge about the context for performing the behaviour rather than the form of the behaviour itself. Conversely, production imitation occurs when "after observing a demonstrator perform a novel action, or novel sequence or combination of actions that is not in the observer's own repertoire, the observer then becomes more likely to perform that same action or sequence of actions." (Hoppitt and Laland 2008, p. 118). Production imitation therefore differs from contextual imitation in that the action or sequence of actions performed was not previously in the observer's repertoire.

Several good examples of contextual imitation can be found in laboratory experiments using *Coturnix japonica* (Japanese quail) and *Columba livia domestica* (white carneaux pigeons) (Akins and Zentall 1996; Kaiser et al. 1997; Zentall et al. 1996). In these experiments a food reward could be achieved by either stepping or pecking on a treadle. The action used by observers to receive this award was found to be dependent on the action previously demonstrated to them by conspecifics.

Evidence for production imitation comes from work by Moore (1992). Moore presented data from a single *Psittacus erithacus* (African grey parrot), which was demonstrated several patterns of behaviour made up of both vocal and motor behaviours, such as waving followed by saying "ciao". The parrot learned to imitate each of these combined

actions, which the author believed highly unlikely to have already been within its repertoire, however this was not tested.

1.1.2.2 Goal emulation

Emulation differs from imitation in that the observer is not copying the actions of a demonstrator but rather the results that the demonstrator achieves. More formally, "Emulation occurs when, after observing a demonstrator interacting with objects in its environment, an observer becomes more likely to perform any actions that bring about a similar effect on those objects" (Hoppitt and Laland 2008, p. 122). A good example of emulation can be found in *Pan troglodytes* (chimpanzees). Whiten (1998) presented the chimpanzees with "artificial fruit" from which three defences had to be removed in order for the chimpanzees to access the food reward contained within. Each defence could be removed by either one of two methods. Whiten discovered that observer chimpanzees were more likely to use the method demonstrated to them, however, the specific action used to complete this method was not necessarily copied exactly, suggestive of emulation rather than imitation.

1.1.2.3. Observational conditioning

Observational conditioning can be thought of as a form of classical conditioning (Heyes 1994), with an observer learning an appropriate response to an object or event in their environment via an association between that environmental stimulus (the CS) and the behavioural response of a demonstrator to this stimulus (the US). The social learning process of observational conditioning can be used to describe the behaviour of young *Macaca mulatta* (rhesus macaques) that adopted a previously absent fear response to snakes on observation of a fear response from their parents (Mineka and Cook 1988).

1.1.2.4 Local enhancement and stimulus enhancement

The term local enhancement was first introduced by ethologist William Thorpe (1956). It was originally defined as "apparent imitation resulting from directing the animal's attention to a particular object or to a particular part of the environment" (Thorpe 1963, p.134). Thorpe's definition can be applied to both local enhancement and stimulus enhancement. Opinion is currently divided on whether or not local enhancement and stimulus enhancement are two separate processes, with some authors classing local enhancement to be the same as or a sub-set of stimulus enhancement (Galef, 1988; Heyes, 1994) and others regarding them as two separate processes in their own right (Zentall, 1996; Hoppitt & Laland, 2008). Stimulus enhancement occurs when the observation of a demonstrator (or its products) increases the probability of an individual being exposed to a stimulus in the environment (or another of its type), with the location of the stimulus being irrelevant. In contrast, local enhancement occurs when observation of a demonstrator (or its products) draws an individual's attention to a particular location, which may or may not be coupled with a stimulus. In both cases the observer, once drawn to the stimulus or location, will subsequently rely on asocial learning to obtain information.

One possible example of stimulus enhancement can be found in a study by Krebs et al. (1972) on *Parus major* (great tits). Krebs et al. (1972) found that individuals would increase foraging effort in a particular type of hiding place (out of four possibilities) after conspecifics were observed to locate food in a similar location. Another example is the milk bottle opening behaviour by *Parus atracapillus* (black-capped chickadees). Sherry and Galef (1984) discovered that upon exposure to a previously opened bottle,

formerly naive birds could learn how to open them without the need for the direct observation of bottle opening behaviour of conspecifics.

Examples of local enhancement include *Gyps spp.* (Old World vultures) circling over a carcass attracting conspecifics to the same location, despite having not seen the carcass themselves (Buckley, 1996) and the presence of *Bombus terrestris* (bumblebees) attracting conspecifics to flowers (Leadbeater and Chittka 2007).

1.1.2.5 Social facilitation

Hoppitt and Laland (2008) describe social facilitation as "when the mere presence of a demonstrator affects the observer's behaviour" (pg. 115). This process has the potential to lead to social learning, for example via a reduction in fear or neophobia facilitating an increased likelihood of interacting with stimuli in the environment. *Cebus capucinus* (Capuchin monkeys) have been shown to have an increased likelihood of consuming a novel food type in the presence of conspecifics rather than when they are solitary, even when those conspecifics are not consuming the novel food themselves (Visalberghi and Adessi 2000). This reduction in fear may then lead to learning, for example by discovering that a novel food is palatable.

1.1.2.6 Response facilitation

Response facilitation is a term introduced by Byrne (1994) to describe a process of social learning in which an observer witnesses a demonstrator performing an act of behaviour and increases the likelihood of the observer performing that behavioural act itself. It has been defined by Visalberghi and Adessi (2000) as ''the increased probability of performing a class of behaviours in the presence of a conspecific performing the same class of behaviors'' (p. 69). Response facilitation may lead to social learning, as by synchronizing behaviour, an animal may learn when and where is

appropriate to perform certain actions (Hoppitt and Laland 2008). A good example of response facilitation comes from a study by Hoppitt et al. (2007). It was observed that *Gallus gallus domesticus* (chickens) would preen at a rate related to the number of conspecifics also preening within the same aviary. However, it is also possible that an outside stimulus unobserved by the experimenter may have facilitated preening in demonstrator and observers.

1.1.2.7 Observational R-S learning

Observational R-S learning can be defined as 'a subset of response-reinforcer learning (R–S) in which observation of a demonstrator exposes the observer to a relationship between a response and a reinforcer at t1, and exposure to this relationship effects a change in the observer detected, in any behaviour, at t2'(Heyes 1994, pg. 225). R-S learning (alternatively known as operant conditioning) has been described above in section 1.1.1.1. Observational R-S learning differs from imitation in that it does not necessarily require the observer to witness the demonstrator being rewarded for its actions. It is conceivable that an observer could learn what not to do as a direct result of watching demonstrators make mistakes (Heyes, 1994; Want and Harris, 1998). However, observational R-S learning would overlap with contextual imitation when the observer's learned response matches that of the demonstrator (Hoppitt and Laland 2008).

It may be feasible to distinguish observational R–S learning from other social learning processes by using a two-action test, where a demonstrator responds to a single stimulus with two different actions with one of the actions observed to be rewarded while the other is not. It would then be possible to confirm if an observer has formed an R-S association if the observer goes on to imitate only the action for which the demonstrator

was rewarded (Hoppitt and Laland 2008). However, to the author's knowledge, no such study has been carried out. There is therefore currently no direct empirical evidence for observational R–S learning.

1.1.2.8 Social enhancement of food preferences

The social enhancement of food preferences can be defined as occurring when "after being exposed to a demonstrator carrying cues associated with a particular diet, the observer becomes more likely to consume that diet." (Hoppitt and Laland 2008, pg. 132) and is discussed in detail in section 4.1.

1.3   Social learning strategies

Relying on social learning to gain information about the environment can often be advantageous, as it allows individuals to avoid all the costs associated with the collection of private information such as exposure to predators and large costs in both energy and time that are common with trial and error learning. However, social learning can also prove to be costly in terms of both time and effort, as well as copying error, and theoretical studies reveal social learning to be costly (e.g. when individuals acquire outdated information) when social learning is used indiscriminately (Boyd and Richerson 1985; Feldman et al. 1996; Giraldeau et al 2002; Laland 2004; Kendal et al. 2005). In order for social learning to be adaptive, individuals must be selective in their use of social learning and use it in combination with sampling the environment via asocial means (Laland 2004). It is therefore expected for natural selection to have favoured psychological mechanisms that dictate under what circumstances individuals should rely on social learning and from whom they should learn (Laland 2004; Rendell

et al. 2010). These mechanisms have been labelled social learning strategies (Laland 2004).

On reviewing a number of formal models, Laland (2004) collated a list of circumstances under which theory suggests fitness would be affected by a reliance on social rather than on individual learning (see also Kendal et al. 2005). Laland (2004) outlined two different types of social learning strategies; *"When" strategies*, which specify the circumstances under which individuals copy others, and *"who" strategies*, which identify from whom individuals learn, as detailed in Figure 1.1. Subsequently, Hoppitt and Laland (2013) added "what strategies" to refer to biases for acquiring particular content (e.g. a fear of snakes) socially.

Social Learning Strategies

"When" Strategies
Copy when established behavior is unproductive
Copy when asocial learning is costly
Copy when uncertain

"Who" Strategies
Copy the majority
Copy if rare
Copy successful individuals
Copy if better
Copy if dissatisfied
Copy good social learners
Copy kin
Copy "friends"
Copy older individuals

Note—"When" strategies specify the circumstances under which individuals copy others, and "who" strategies identify from whom individuals learn. Here, the term *copy* refers to any form of social learning.

Figure 1.1: The different social learning strategies. Taken from Laland 2004 (pg. 5).

1.3.1 Empirical evidence for social learning strategies

A comprehensive review of the literature regarding the evidence for each social learning strategy, which now runs to hundreds of papers, is beyond the scope of this thesis. The

purpose of the following section is more to provide the reader with illustrative examples of a handful of different strategies. For a more detailed review see Laland (2004) and Hoppitt and Laland (2013).

1.3.1.1 "When" Strategies

1.3.1.1.1 Copy-when-established-behaviour-is-unproductive

If a particular behaviour an animal is engaged in is not producing the desired consequences, it would likely be beneficial to switch to whichever behaviour others in the locality are performing. Evidence has been found in pigeons and bees to support the existence of this strategy.

In a study by Lefebvre and Palameta (1988), white corneaux pigeons were presented with a foraging task in which they could access seed by pecking open a carton. The authors found that the pigeons' first port of call was to scrounge seed from the success of others and that they would only switch tactic to solving the task and producing food once scrounging became unproductive due to the limited number of producers. Previous experimental analyses had established that asocial learning of the task was unlikely, therefore social learning of the producer strategy can be assumed (Lefebvre and Palameta 1988).

When foraging, *Apis mellifera* (honeybees) will use their own private information about successful foraging locations in preference to spatial information provided by dancers (Grüter *et al*. 2008). However, if their previous foraging trip based on private information was unsuccessful, they will switch to the location mapped out by the dancers (Biesmeijer & Seeley 2005).

1.3.1.1.2 Copy-when-asocial-learning-is-costly

When personal information is difficult or costly to acquire, it is logical for an individual to take advantage of the comparatively cheap social information (Boyd and Richerson 1985). Examples for the use of this strategy are found across a range of taxa. Templeton and Giraldeau (1996) conducted a study on the foraging behaviour of *Sturnus vulgaris* (European starlings). It was found that the starlings would rely on social information (in this case, public information) only when personal information about relative patch quality was difficult to acquire.

Further evidence for the use of this strategy can be found in an experiment by Webster and Laland (2008). *Phoxinus phoxinus* (European minnows) were presented with two prey patches under differing levels of predation risk. These prey patches were identical in every respect except for whether or not conspecifics were present (i.e. socially demonstrated or non-demonstrated) under a demonstration phase. When tested in the absence of demonstrators, it was discovered that, regardless of whether observers had received no prior experience or even conflicting experience of the prey patches, they spent a significantly higher proportion of time in the demonstrated over the non-demonstrated prey patch when simulated predation risk was high than when predation risk was low.

Bumblebees also show evidence of using a copy when asocial learning is costly strategy. Saleh *et al*. (2006) have shown that bees that forage from more complex flowers with greater associated time costs are much more likely to rely on social learning than bees that visit simpler flowers, using conspecific scent marks to identify productive flowers.

1.3.1.1.3 Copy-when-uncertain

Theoretical models have assumed that animals should rely on their own experience (private information) when relatively certain about the properties of their environment, but should rely more heavily on social information when less certain (Boyd and Richerson 1985; 1988). There are a number of empirical studies that provide evidence for this assumption. For example, Templeton and Giraldeau, (1995) discovered that European starlings will use social information with regards to foraging locations (determined by colour association), but only when they themselves possess no personal information. If individuals possessed prior, conflicting, knowledge as to the location of food, social information was ignored.

Galef et al. (2001) also provides evidence for a 'copy when uncertain' strategy in *Rattus norvegicus* (Norway rats). The focus of this study was kleptoparasitism, with regards to the stealing of food from conspecifics, despite there being a surplus. It was discovered that rats were significantly more likely to steal food from others when they had no prior experience of the food that was presented to them in comparison to those that had experienced prior exposure to the food. It is apparent therefore that when uncertain about the safety of a novel food type, rats will use social information to determine which food items are safe to consume.

A further study on Norway rats by Galef et al. (2008) made a comparison of the food preferences of rats that were certain or uncertain about the safety of two foods. Certain or uncertain rats were determined by inducing illness into rats (by injecting lithium chloride) directly following the consumption of either one or two novel food flavours (cinnamon and/or cocoa). Those that had consumed only 1 novel flavour had reason to

be certain as to the cause for their illness, however, rats that consumed two novel flavours immediately prior to becoming ill could have been so due to either, or a combination, of both foods. Once recovered, both the certain and uncertain rats were allowed to interact with a demonstrator which had recently consumed one of two additional novel flavours. When later given the choice between the two additional flavours, uncertain rats were significantly more likely than certain rats to consume the same flavour as their demonstrator than certain rats.

1.3.1.2 Who strategies

1.3.1.2.1. Copy-the-majority

Theoretical analyses have revealed that a conformist approach to social learning (i.e. disproportionately copying the majority behaviour) is favoured in most circumstances where social learning has the potential to be evolutionarily adaptive (Boyd and Richerson 1985). Such findings suggest that a 'copy the majority' strategy should be abundant in animal social learning. Whilst few empirical studies have addressed this question directly, there is evidence for the possibility of conformist social learning (Brown and Laland 2002). The probability of an individual adopting a behaviour, or pattern of behaviour, has been shown to increase in proportion to the number of individuals already exhibiting that behaviour across a range of species, including *Poecilia reticulata* (Trinidadian guppies) (Sugita 1980; Laland & Williams 1997; Lachlan et al. 1998), Norway rats (Beck & Galef 1989; Chou and Richerson 1992), and white corneaux pigeons (Lefebvre & Giraldeau 1994). However, whilst these studies are consistent with the idea of conformity, they do not provide direct evidence for it.

Day et al. (2001) tested the foraging ability of differing shoal sizes of guppies by hiding patches of food in an aquarium. Individuals in larger shoals located food within a

shorter time frame than those in smaller shoals and conspecifics were attracted to foraging patches with a large number of conspecifics faster than those with small aggregations. However, a 'copy the majority' strategy has been shown to not necessarily be conducive to adaptive behaviour since it hinders the spread of rare behaviour with higher fitness. Day et al. (2001) went on to test the foraging ability of different shoal sizes when individuals were required to break visual contact with the remainder of the shoal in order to find food. In this instance smaller shoals were observed to locate food faster than larger ones, as the proportion of conspecifics remaining was much higher in the larger shoals. If individuals were taking a conformist, 'copy-the-majority', approach, as seems to be the case, when in larger groups, they would copy the behaviour of the largest proportion of the shoal and remain in their location rather than break away from the rest of the shoal.

1.3.1.2.2. Copy-successful-individuals

Social learning will undoubtedly be more effective when adopting the same behaviours as the more successful members of the population (Laland 2004). Successful individuals could be identified by a range of cues, such as reproductive success, hunger state or health. Successful individuals may also include high-status individuals if there is a social hierarchy.

Empirical evidence for the use of a 'copy successful individuals' strategy can be found in a range of taxa. For example, in nursing colonies of *Nycticeius humeralis* (evening bats), adult females, unsuccessful during a previous foraging trip, would subsequently follow successful individuals (Wilkinson 1992). It was also discovered that those previously unsuccessful females that engaged in a 'copy successful individuals' strategy were subsequently more successful than those that foraged alone (Wilkinson 1992).

Menzel (1974) conducted a study in which it was discovered that naive foraging chimpanzees were more likely to follow a conspecific with knowledge as to the location of food than they were to follow an uninformed conspecific. Fish have also been shown to follow informed individuals to a food source, with evidence from guppies (Lachlan et al. 1998) and *Notemigonus crsoleucas* (golden shiners) (Reebs 2000), whereby previously trained, informed, individuals were able to lead shoals of naive individuals toward a specific corner of the tank in which food was made available.

Further examples of a 'copy-successful-individuals' strategy can be found in the nest-site decisions of some insects and birds (Sarin and Dukas 2009; Seppanen et al. 2011; Forsman and Seppanen 2011). For example, *Ficedula hypoleuca* (pied flycatchers) copied the nest-site choices of successful heterospecific *Periparus ater* (coal tits) and *Cyanistes caeruleus* (blue tits), but were observed to avoid nesting in locations where coal tits and blue tits had low numbers of chicks (Seppanen et al. 2011; Forsman and Seppanen 2011).

A study by Sarin and Dukas (2009) revealed that female *Drosophila melanogaster* exhibited a stronger preference for laying their eggs on a particular type of novel food after experiencing that food alongside other females who had laid eggs on that food compared with females that had experienced the same novel food alone.

1.4   Social learning in fish

The cognitive capabilities of fishes have historically been underestimated, and in many respects their intellectual faculties are comparable to birds and mammals (Laland et al. 2011). The belief that animal intelligence mirrors the degree of relatedness to humans

has become outdated, with the view of convergent evolution in distinct taxonomic groups becoming more popular (Shettleworth 2001; Emery and Clayton 2004). There is now extensive experimental evidence that social learning is a key aspect in the behavioural development of many fish species (Brown and Laland 2003; Laland et al. 2011).

Most species of fish are social animals and form shoals or small groups at some stage of their life cycle, with the behaviour of conspecifics (and in some cases, heterospecifics) providing an invaluable source of information with regards to a variety of biologically important decisions, such as the identity of predators and relevant predator-avoidance tactics, whom to mate with and where to deposit eggs, what to eat and where and how to access it, and many other challenges (Laland et al. 2011).

Using fishes for the study of social learning has several practical advantages over other vertebrate species. The diffusion of information and innovations are group-level phenomena and require not just replicate animals, but replicate populations of animals if they are to be studied reliably (Laland et al. 2011). It is logistically difficult and expensive to address the practicalities of assembling large numbers of populations of replicate primates or cetaceans, but very simple and comparatively cheap to achieve this with small fishes in controlled laboratory conditions. For example, sticklebacks are widespread throughout the temperate Northern Hemisphere and easily captured and maintained in the laboratory in simple aquaria.

Researchers using fish to study social learning therefore benefit from the multiple (controlled) conditions expected of good experimental design and good statistical

power, bringing experimental rigour to any social learning investigation (Laland et al 2011).

Below I give a review of the evidence for social learning in fishes under the contexts of mate choice copying, migration and orientation, foraging, anti-predator behaviour, and aggressive interactions.

1.4.1 Mate choice copying

Mate choice copying can be defined as an individual selecting a partner because others of the same sex have selected that individual as a partner previously (Gibson & Hoglund 1992). Social learning has been shown to influence mate choice in several species of fish including *Pomatoschistus microps* (common gobies), (Reynolds and Jones 1999), guppies (Dugatkin 1992; Dugatkin and Godin 1992, 1993; Briggs et al. 1996; Godin and Hair 2009), *Oryzias latipes* (Japanese rice fish) (Grant and Green 1996), *Gasterosteus aculeatus* (threespined sticklebacks) (Ridley and Rechten 1981; Goldschmidt et al. 1993), *Cottus gobi* (European bullheads) (Marconato and Bisazza 1986) and *Poecilia latipinna* (sailfin mollies) (Schlupp et al. 1994; Sclupp and Ryan 1997; Witte and Ryan 1998, 2002).

Perhaps the most widely known example of mate choice copying is in the guppy. Dugatkin (1992) conducted a series of experiments using wild caught Trinidadian guppies. Two males were secured at either end of an aquarium, with a model female residing near one of the males. A focal female was then placed into the middle of the tank and allowed to observe the males. After the model female was removed, the focal female was then allowed to swim freely within the aquarium during which time it was observed that focal females would spend a significantly larger amount of time with the male that had been near to the model female. This significance was upheld even when

the male's locations were reversed after the observation period (Dugatkin 1992). Dugatkin and Godin (1992) then went on to demonstrate that the mate preference of another female guppy was influential enough to reverse previous mate choice preferences. A further study by Dugatkin and Godin (1993) revealed the interesting finding that female guppies will copy the mate choice of larger (and therefore likely to be older) females, whilst the previous mate choice of smaller females had no effect. Witte and Ryan (2002) carried out mate choice trials on both male and female sailfin mollies similar to the original experiment undertaken on guppies by Dugatkin (1992). However, the trials by Witte and Ryan (2002) were implemented in-situ in the Comal River, New Braunfels, Texas. Mate-choice copying is therefore known not simply to be an artefact of the laboratory (Witte and Ryan 2002), at least in sailfin mollies.

Mate choice copying has also been shown to occur between species. *Poecilia formosa* (the Amazon molly) is a species consisting entirely of females which reproduce clonally, however, they are reliant on the sperm of heterospecific males, in this case sailfin mollies, to initiate embryogenesis (Ryan 1997). Mating with gynogenetic species should incur no benefit to the male and therefore reduce the male's fitness due to both energy costs from courting and time costs taken away from courting female conspecifics. Male sailfin mollies have been shown to be able to distinguish between females of their own species and Amazon mollies. However, the continued existence of Amazon mollies suggests that sailfin molly males incur a benefit from such interactions (Schlupp et al. 1994). These benefits were identified by Schlupp et al. (1994) when they showed that female Amazon mollies will copy the mate choice of sailfin mollies. Males therefore increase their attractiveness to conspecific females by mating with the heterospecific gynogens.

1.4.2 Migration and orientation

For most fish species, biologically important locations, such as profitable foraging sites, areas safe from predators and suitable areas in which to find mates and reproduce, are all subject to environmental variation. Information as to the location of such areas can therefore not be entirely inherent and must be learned. Many fishes are now known to exhibit traditionality in their use of mating sites, preferred schooling sites, resting sites, feeding sites and pathways through their natural environments (Brown and Laland 2003; 2006). A straightforward method for acquiring knowledge of the location of important resources is simply to follow others and in the process to learn the site or route for themselves.

There are several experiments in which it has been demonstrated that an individual fish will follow another. For example, Reebs (2000) showed that a minority of informed golden shiners were able to lead a shoal of naïve conspecifics away from a preferred darker area of the tank to an expected food source. Kohler (1976) demonstrated a similar phenomenon in *Cyprinus carpio* (common carp). A single trained individual was able to lead up to 10 conspecifics to a feeding tube in response to an acoustic stimulus. Even though this is clear evidence of informed individuals leading uninformed conspecifics to a resource, it does not signify social learning, as there is no evidence that the naïve conspecifics could remember the route or signal and relocate the resource by themselves. However, Helfman and Schultz (1984) have indicated social learning of this type. They showed that transplanted *Haemulon flavolineatum* (French grunts) could learn the daily migration route between the foraging and resting sites used by resident conspecifics. The transplanted individuals only needed to follow the informed residents

twice before being able to navigate the route themselves in the absence of all previous residents.

Migratory traditions have also been shown to be present in *Thalassoma bifascatum* (bluehead wrasse), which have mating-site locations that remain in place over many generations. When entire populations were removed and replaced with transplanted populations, the wrasse were observed to establish new mating sites, which remained constant over the 12 year period of the study (Warner 1988). However, when Warner replaced newly established populations after one month, he found the introduced fish reused the same sites as their immediate predecessors (Warner 1990). Thus, these sites are not fully determined by habitat structure; rather, Warner's findings suggest that site use is initially based on resource assessment but then preserved through social learning.

The use of social learning to acquire knowledge of a route to a resource has also been shown to occur under laboratory conditions. Laland and Williams (1997) trained individual guppies to follow a particular route (out of two alternatives) to a food source. After being placed in the experimental aquarium with the demonstrators once a day for 5 days, it was apparent that the observers showed a significant preference for the route demonstrated to them and consistently chose to follow this route to a food source in the absence of a demonstrator, despite there being an alternative route of equal distance and complexity. Laland and Williams (1998) then went on to demonstrate the surprising level of influence these social cues impart. They used a transmission chain design, where small shoals were trained to take one of two routes, of which one route was substantially longer and therefore more energetically costly. These trained founders in each group were then gradually replaced by naïve individuals. After three days with no

original founders in the groups, the more costly route was still being utilised by those groups with founders that were trained to use it.

1.4.3 Foraging

Social learning is also a means by which fishes increase their foraging efficiency (Brown and Laland 2006). For instance, when a fish discovers a food patch, the foraging behaviour of that individual will frequently attract others to the same area. Fish also often appear attuned to the feeding movements of others. For example, juvenile *Salmo salar* (Atlantic salmon), dart to the water's surface to catch prey items from their benthic foraging stations. This darting motion is used as a cue by conspecifics that indicate food is available (Brown and Laland 2002). Juvenile *Dicentrarchus labrax* (European sea bass), after observing trained conspecifics press a lever to gain a food reward, subsequently learned this behaviour themselves (Anthouard 1987). Fishes do not just learn of the location of food socially, but have been found to learn novel food types (Brown and Laland 2001, 2002) as well as to acquire novel foraging behaviour. A striking example of the latter is provided by Schuster et al. (2006), who demonstrate experimentally that *Toxotes jaculatrix* (archer fish) can learn to shoot down moving aerial prey through observation of the successful performance of conspecifics.

1.4.4 Anti-predator behaviour

Fishes also learn anti-predator behaviour from conspecifics. One mechanism by which this can be attained in fishes is via a chemical cue, known as Shreckstoff, released as a result of damage to the skin (Von Frisch 1938) or, in some species, voluntarily, as 'disturbance pheromones' (Wisenden et al 1995). When these cues are detected by conspecifics, or heterospecifics, the receivers typically exhibit an anti-predator response (Brown and Godin 1997). Extensive experimental evidence, in multiple species, has

established that fish can learn the identity of predators through associating predator cues with the detection of Schreckstoff released by other fish. For instance, Hall & Suboski (1995) found that control of the alarm reaction could be transferred to previously neutral stimuli via paired conditioning and could provide a mechanism whereby naive animals learn to recognize predators without ever coming into direct contact with them. Similarly, Chivers & Smith (1994) demonstrated that minnows could associate these alarm substances with chemical cues emanating from predators. Minnows also learn to exhibit anti-predator behaviour in response to olfactory cues from a novel predator when these cues are received at the same time as seeing a fright response from conspecifics (Suboski et al. 1990). They can associate spatial areas, and even chemical cues associated with the water, with predator risk through the same mechanism (Chivers and Smith 1995), allowing fishes to recognize habitats with high predation risk. Chivers & Smith (1994) and Suboski et al. (1990) recorded that naive minnows (*Pimphales promelas*) and *Danio rerio* (zebra danios), respectively, receiving visual cues of a fright response from demonstrators through a clear barrier, acquire anti-predator responses to predator cues, if experiencing them simultaneously. It is also known that the observed fright behaviour of one individual will induce a similar response in others despite them having not seen the predator themselves (Krause 1993a). This phenomenon is known as the 'Trafalgar effect' (Treherne and Foster 1981). Shoaling fish are therefore made aware of a potential predator earlier than they would if solitary and the shoal can respond to the threat more effectively with coordinated evasion behaviour (Krause 1993a). Magurran & Higham (1998) discovered that minnows, even though unable to see the predator, exhibited predator avoidance behaviour upon observing the fright reaction of conspecifics to a model pike.

1.4.5   Aggressive interactions

Social learning also allows fishes to learn about the fighting potential of rivals. By exploiting signals communicated between others, known as 'eavesdropping' (McGregor 1993), individuals can gain valuable information about the fighting ability and social status of others without the risk of engaging in contests themselves. Such behaviour has been observed in several species of fish, for example male *Xiphophorus helleri* (green swordtails) were less likely to initiate or escalate fights against others they had previously observed winning contests (Early and Dugatkin 2002). Oliviera et al. (1998) also found that male *Betta splendens* (Siamese fighting fish) use information gleaned from the observation of aggressive interactions between neighbouring conspecifics to subsequently guide their own fights. In a study by Grosenick et al. (2007), it was reported that males of *Astatotilapia burtoni* (a cichlid species), base their decisions on which conspecific males to fight following the observation of fights between rivals. By observing the fights of others, the cichlids are able to use indirect social cues to make inferences on the hierarchy.

1.5   Broader comparative perspective

Despite the large volume of evidence for various social learning mechanisms being utilised by fish under a variety of contexts, there are still extensive gaps in research, which the experiments in this theses aim to go some way toward filling. There are several contexts under which the use of social learning has not been examined. Predation is a significant threat to a wide variety of fish species, with many species being predated upon by a variety of taxa. Whilst some predator evasion techniques have been studied in fish under a social learning context, such as the use of Shreckstoff as an alarm pheromone (e.g. Hall & Suboski 1995), to the author's knowledge, social learning

with regards to shelter location and selection has not. In fact, studies into the social learning of shelter choice have been undertaken in only a single genus; *Panuliras* (spiny lobsters) (e.g. Briones-Fourzan et al. (2008) and Childress & Herrnkind (1997; 2001)). This thesis aims to go some way in bridging this gap in research in Chapter 3.

Whilst there is substantial evidence in the ability of a variety of fish species to use social learning under a foraging context, there are still a number of social learning mechanisms that have not been addressed under this context. One such mechanism is the social enhancement of food preferences (see sections 1.1.2.8 and 4.1). All of the studies into this form of social learning have focused on mammals and most extensively in rodents (Galef et al. 1983; Galef & Wigmore 1983; Galef 1988; Valsecchi et al. 1996; Lupfer et al. 2003; Galef 2005; Ratcliffe & ter Hofstede 2005; Lupfer-Johnson & Ross 2007). There are no published studies that have studied the social learning mechanism of the social enhancement of food preferences in fish. The experiments in Chapter 4 therefore go some way in filling this gap in research.

In addition to understanding the social learning mechanisms and strategies used by fishes, another key element to understanding the evolution and utilisation of social learning is to examine the pattern of diffusion of social information through populations. This can be achieved through the study of a population's social network and the adoption of novel behavioural traits (discussed in detail in chapters 5 – 7). However, the study of social network structure in non-human animals, has only recently received attention and there is much research in the area still required. The experiments in Chapters 6 and 7 use Network Based Diffusion Analysis (NBDA), a new approach to

analysing social network data and the diffusion of information within networks to help add to the limited number of papers on fish in this area.

1.6 Summary

In summary, there are a number of different processes by which social learning can occur, evidence for which can be found across a wide range of taxa. In order to be adaptive, the use of these social learning processes cannot be employed indiscriminately, but rather in a more strategic manner, with many different social learning strategies depicting when and from whom individuals should acquire and utilise social information. There is a host of evidence to suggest that there are a variety of contexts under which fish are able to employ these processes and strategies.

Chapter 2 leads on to discuss the characteristics of one particular species of fish, the threespined stickleback. This species is the focus test species for this thesis, reasons for which shall also be discussed.

Chapter 2. The threespined stickleback

In this chapter I briefly outline the general background and characteristics of my study species, the threespined stickleback. Topics include the phylogeny and natural history of the species, their global distribution, morphology, and basic ecology. I then go on to discuss the threepined stickleback as a model species, their merits in the laboratory, and previous examples of the utilisation of threespined sticklebacks in the study of social learning.

2.1 Phylogeny and natural history

The threespined stickleback belongs to Gasterosteidae, a family of small teleost fishes with 5 genera and 16 species (Barber and Nettleship 2010), the closest related of which are shown in Figure 2.1. The UK is host to three of these species; the threespined, *Pungitius pungitius* (ninespined stickleback) and *Spinachia spinachia* (fifteenspined stickleback) (Barber and Nettleship 2010).
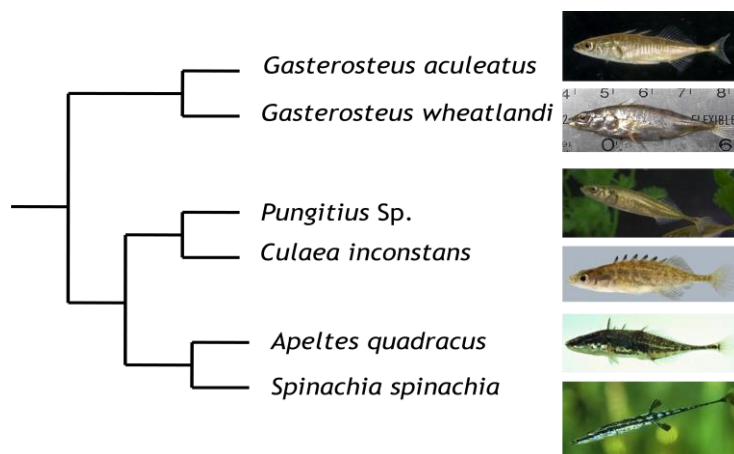
Figure 2.1: Stickleback phylogeny as per Kawahara et al. (2009)

Threespined stickleback have been found in marine fossil deposits dating back 10 million years and do not significantly differ from extant marine populations (Bell 1994).

Repeated colonisation of these marine threespined sticklebacks into freshwater lakes and rivers characterises the natural history of the species. Colonisation episodes often followed glacial retreat, with marine threespined sticklebacks invading newly created freshwater habitats, establishing freshwater and anadromous populations throughout North America, Europe and Asia (McKinnon and Rundle 2002). Inland populations in Northern Europe were founded as little as 8,000 – 10,000 years ago (Barber and Nettleship 2010). Once new populations were established, there were relatively high levels of morphological, behavioural and physiological divergence as a result of adaptation to a variety of selection pressures in freshwater and anadromous habitats, explaining the high level of diversity found across freshwater populations of threespined sticklebacks today.

2.2 Geographical distribution

Threespined sticklebacks have a wide geographical distribution, found throughout much of the northern hemisphere, specifically around the margins of the Atlantic and Pacific oceans (Bell 1994). See Figure 2.2 for a detailed distribution.

Figure 2.2: Map showing the global distribution of the threespined stickleback (shaded areas). Adapted from McKinnon and Rundle (2002, pg. 481).

Populations can be solely marine, anadromous, or solely freshwater (Bell 1994). The diversity of habitats in which the threespined stickleback resides is far greater than that of most fish species (Reimchen 1994). Threespined stickleback are found across a wide range of differing aquatic habitats, including small ponds, littoral, benthic, and limnetic lake habitats, streams and rivers, estuaries, tidepools and even the open ocean (Reimchen 1994).

2.3 Morphology

The threespined stickleback is typically a small fish, with a mean standard length of 5cm. General body shape is streamlined but with a large pectoral fin. The threespined stickleback is well protected from predators, possessing bony armoured lateral plates forming a single row along each side of the body and 3 dorsal spines, the first two of which are large and serrated. As well as dorsal spines, the threespined stickleback also possesses two pelvic spines, one on either side of the body (Bell 1994). The dorsal and pelvic spines can lock into an erect position when the fish is threatened, which along with the armour plating help protect against predation.

There is significant morphological variation between habitats and populations, particularly with regards to the armour plating. Additional significant variations include body depth and dorsal spine length. Body colour of the threespined stickleback also varies with habitat and geographical location. As a general rule, they are cryptically coloured in varying shades of green and brown. During the reproductive season males will adorn a blue eye and a blue tinge to the body with a bright red throat, often extending along the abdomen.

2.4 Ecology

2.4.1. Prey

The diet of the threespined stickleback is highly dependent upon the habitat in which it resides. Populations differ in morphology according to habitat, in part due to adaptations or plastic responses to differing feeding regimes. Perhaps the most striking example of adaptation to differing prey items can be seen in the benthic/limnetic divide as documented by McPhail (1984). Benthic sticklebacks, with a larger jaw, feed on invertebrates from the lake bottom, whilst limnetic populations have adapted to feeding on zooplankton, with a greater number of gill rakers to trap fine prey (Hart and Gill 1994). In general, threespined sticklebacks predate upon a wide variety of invertebrate prey species.

2.4.2. Predators

Their abundance, wide ecological diversity, small size and slow swimming speed makes the threespined stickleback accessible as prey to a large number of piscivorous predators, despite their armoured defences. There are at least 68 species of known predator to the threespined stickleback from 7 major taxa (for a detailed list see Reimchen 1994). These include other species of fish, such as *Esox spp.* (pike), *Perca spp.* (perch) and *Salmo spp.* and *Oncorhynchus spp.* (salmonids), avian predators, such as grebe, heron and kingfisher, and even some macroinvertebrate species (Reimchen 1994). Cannabilism is also common, with adult conspecifics consuming fry and eggs (Foster 1988).

2.4.3. Reproduction

In spring males migrate to the breeding grounds where they establish territories, build nests from a variety of materials, and court females. Once the females have laid their

eggs in the nest of their chosen males, they have no participation in the rearing of young. There is however, an extensive level of paternal care whilst the eggs are developing. The male will continually oxygenate the eggs during the development process by fanning currents of water over the eggs with their pectoral fins and remove any eggs from the nest that are dead or diseased. Males will also guard their eggs from predators, including conspecifics (Whoriskey and FitzGerald 1994).

An alternative mating tactic also exists, with some males opting for sneaky matings. Sneaking males do not adopt the bright colouration usually seen in males during the breeding season, but instead are drab and inconspicuous. Sneaking behaviour typically follows a pattern of freezing, sinking to the bottom of the water column, and slowly approaching the nest of a courting male. If the sneaker remains undetected by the courting male, they will enter the nest directly after the female and fertilise the eggs (Foster 1994).

2.5 Threespined sticklebacks as a model species

The threespined stickleback has been used to address a wide range of questions throughout many biological fields including behaviour, morphology, physiology, evolution, and ecology (Kingsley and Peichel 2007). The enormous diversity of freshwater populations enables evolutionary biologists to study the ecological basis of adaptive radiation and phenotypic variation (Barber and Nettleship 2010). A genome-wide linkage map for the threespined stickleback was published by Peichel et al. (2001), followed by the publication of the full genome sequence in 2006 (www.ensembl.org/Gasterosteus_aculeatus/index.html), enabling a plethora of research into the genetic basis of intra-specific diversity (Barber and Nettleship 2010).

One of the founders of modern behavioural biology, Niko Tinbergen, first started working on the three-spined stickleback in the 1930s (Huntingford and Ruiz-Gomez 2009). Since then extensive study into behavioural biology using the threespined stickleback has been undertaken in a variety of contexts including foraging (Milinski and Heller 1978; Mackney and Hughes,1995; Gill and Hart 1998; Salvanes and Hart 1998; Araujo *et al*., 2008), shoaling (Bumann and Krause 1993; Krause and Tegeder 1994; Barber, 2003; Ward *et al*., 2004a; Frommen and Bakker 2004; Frommen *et al*. 2007a), personality (Ward *et al*., 2004*b* ; Pike *et al*., 2008; Ioannou *et al*., 2008), and sexual signalling (Milinski and Bakker 1990; Candolin, 1999; Kraak *et al*., 1999) (For a complete review see Huntingford and Ruiz-Gomez 2010).

The species can be successfully bred in the laboratory and can be reared and maintained as adults in small group sizes. They adapt well to laboratory conditions, exhibiting their full behavioural repertoire (Barber and Nettleship 2010). The species' popularity and diversity of uses has established the threespined stickleback as a biological 'supermodel' (Gibson 2005).

2.6 Social learning in sticklebacks

As discussed in section 1.4, the cognitive capabilities of fishes have historically been underestimated, and in many respects their intellectual faculties are comparable to birds and mammals. There is now extensive experimental evidence that social learning plays an important role in the behavioural development of many fishes.

Threespined sticklebacks and their closely related counterpart, the ninespined stickleback (see Figure 2.1) have been repeatedly demonstrated to possess a tendency

for social learning which, along with their suitability for behavioural studies in the laboratory, makes them an excellent species in which to study social learning. Below I give a brief outline of the evidence of social learning in sticklebacks under a number of different contexts.

2.6.1. Foraging

Threespined sticklebacks have been shown to rely on social cues to locate prey via the social learning process of local enhancement. Gotceitas & Colgan (1991) presented groups of 6 adult female threespined sticklebacks with two food patches of unequal profitability. When allowed free access to the food patches, the fish distributed themselves according to the ideal free distribution model (Fretwell and Lucas 1970). However, when the experiment was repeated with individuals prevented from gaining private information about patch quality, individuals selected the food patch with the greater number of conspecifics, regardless of food availability.

In a similar study by Webster and Hart (2006a), threespined sticklebacks were allowed to develop foraging preferences for one of two experimental sub-habitats after prey availability was manipulated. Once established, these foraging preferences persisted regardless of experimental prey availability, suggesting individuals were relying on previously acquired foraging information. However, when presented with social information, focal individuals relied on local enhancement cues rather than prior personal information to select foraging sites.

Webster et al. (2013) compared the effect of open and structured habitat structure on the transmission of foraging information through shoals of threespined sticklebacks. It was established that the location of foraging patches was not greatly affected by social

transmission in an open habitat, however, there was strong evidence that social transmission occurred in a structured habitat and moreover that the transmission of information regarding the location of foraging patches followed the network structure of the shoals (Webster et al. 2013).

Coolen et al. (2003) were able to demonstrate that ninespined sticklebacks are capable of utilising public information in a foraging context. Public information use is the collection of information about the relative quality of a resource by monitoring the success of others (Valone 1989). Observer fish were secured in a central compartment and allowed to observe two groups of demonstrators being fed through artificial feeders at different rates. The set-up was arranged so that the observer could not see the actual food items, only the reactions of the demonstrators to the food. After observing the demonstrators feeding for a period of ten minutes, all demonstrators and remaining food items were removed from the tank and the observer was released and allowed into all sections of the test tank. The observers spent a significantly larger proportion of time in the feeding zone of the demonstrator group that was fed at the faster rate, thus they were able to use the behaviour of the demonstrators to establish which of the two foraging patches was the more profitable.

Coolen et al. (2003) then went on to discover that although threespined sticklebacks and ninesined sticklebacks are a closely related and often co-occurring species, threesined sticklebacks show no evidence of utilising public information in the same context. The hypothesis from Coolen et al. (2003) for this species difference in public information use is that threespined sticklebacks possess greater armour, in the form of lateral plates and longer dorsal spines (Fitzgerald and Wooton 1996) this difference in armour is to such an extent that piscivorous fishes have been shown to display a predatory

preference for ninespined sticklebacks over threespined sticklebacks (Hoogland et al. 1957). The superior defences of threespined sticklebacks mean that they are more likely to withstand the higher predation risk associated with personal sampling and therefore benefit more from maximizing their opportunities to feed. Ninespined sticklebacks however, are more vulnerable to predation and will therefore benefit from observing the success rate of others and only leaving an area of relative safety when high patch profitability is assured. Coolen et al. (2003) also demonstrated that ninespined sticklebacks are not only capable of utilising public information in a foraging context from conspecifics but from the heterospecific threespined stickleback as well.

2.6.2. Anti-predator behaviour

As discussed in section 1.3.4., fishes learn anti-predator behaviour from conspecifics via a chemical cue, known as Shreckstoff, released as a result of damage to the skin (Von Frisch 1938). Threespined sticklebacks have also been shown to possess the ability to detect and respond to Shreckstoff. Brown and Godin (1997) exposed individual threespined sticklebacks to Shreckstoff from a variety of sources; conspecifics belonging to the same population, conspecifics belonging to a different population, *Apeltes quadracus* (fourspine sticklebacks), a closely related species, and green swordtails, a distantly related species not known to possess alarm pheromones. Focal threespined sticklebacks were observed to exhibit a significant increase in anti-predator behaviour when exposed to the skin extract of both conspecific populations and of the fourspine sticklebacks, not to swordtail skin extract (Brown and Godin 1997).

2.6.3. Mate choice

Several studies have shown that female threespined sticklebacks prefer to spawn in nests that already contain eggs (Ridley and Rechten 1981; Goldschmidt et al. 1993).

36

One possible function for this behaviour is mate choice copying, the presence of eggs already present in a nest signifying the mate choice of a previous female and therefore a high quality male. Another possible explanation is that a female may prefer to spawn in a nest that already contains eggs in order to increase egg survival rate (Jamieson 1995). A large number of eggs in one nest reduces predation risk through a dilution effect and paternal care and subsequent offspring survival have been shown to increase in relation to the number of eggs in a male's nest (Sargent 1988).

In natural populations, it is highly likely that female threespined sticklebacks have the opportunity to observe the mate choices of other females (Patriquin-Meldrum and Godin 1998). Females have been observed to visit males in pairs (Wootton 1976), and in high-density populations, females are likely to view several courting males and their nests simultaneously (Whoriskey and FitzGerald 1994).

A study by Patriquin-Meldrum and Godin (1998) examined mate choice copying by female threespined sticklebacks in terms of courtship displays. Using a setup similar to that of Dugatkin's mate choice experiment on guppies (1992), females were presented with two males that had similar body lengths, nuptial colors, parental status, courtship behaviour rates, nests, and territory sizes. Patriquin-Meldrum and Godin (1998) observed that only 62.9% of focal females showed a mating preference for the male that they had previously observed being courted by another female, not sufficient for a significant result. This suggests mate choice copying is not the underlying reason for spawning in nests already containing eggs. However, this study based mate choice selection on courting behaviour only. Females did not have access to males' nests in which to spawn, which may be a crucial element in determining mate choice selection.

2.6.4 Cooperation

Milinski et al. (1990) have shown that cooperation also has the potential to be influenced by social learning in threespined sticklebacks. Focal individuals were observed to swim closer to a predator when they observed (through a one-way mirror) a conspecific 'cooperator' swim up to the predator than when they observed a conspecific 'defector' swim only halfway. After four repeated experiences with both the 'cooperator' and the 'defector', the focal fish continued to swim up to the predator and cooperate with the 'cooperator' even when the 'cooperator' defected, suggesting the focal individual was able to learn and recall which of the two conspecifics were more likely to cooperate.

2.7 Summary

Threespined sticklebacks are a widespread and common species. Repeated invasions of marine populations into newly-formed freshwater habitats resulted in a high level of morphological, behavioural and physiological diversity. The species feeds upon a wide variety of prey and are preyed upon by a wide variety of predators. The threespined stickleback is used widely in biological research and has become a model species, for which the entire genome has been mapped. The species has been used repeatedly in the study of animal social learning, with evidence of their ability to learn socially available under a variety of contexts, including foraging, anti-predator behaviour, mate choice, and cooperation.

The next chapter, Chapter 3, is the first of 4 data chapters. In this chapter both threespined and ninespined sticklebacks were used to assess the use of delayed local enhancement under a shelter choice context.

Chapter 3. Threespined sticklebacks and ninespined sticklebacks don't use delayed local enhancement in a shelter choice assay

3.1 Introduction

Shelter selection is a critical component of the behaviour of most mobile organisms, allowing them to avoid adverse physical and biotic environmental conditions (Schwarzkopf and Alford 1996). For example, a shelter has the potential to provide protection from predation (Manicom et al. 2008), assist in the regulation of homeostasis (Houseal and Olson 1995), avoidance of being displaced by flowing air or water (Pardo and Johnson 2006), and provide protection from dessication (Schwarzkopf and Alford 1996).

The social learning process of local enhancement can influence the behaviour of individuals under a wide range of different contexts, from foraging locations to mate choice. Local enhancement has been shown to influence shelter choice across a range of taxa, as the presence of conspecifics can guide individuals toward refuges and thereby improve refuge search efficiency, and thus reduce exposure to predators (Eggleston and Lipcius, 1992; Childress and Herrnkind, 1997, 2001). For example, Briones-Fourzan et al. (2008) demonstrated that *Panulirus guttatus and P. argus* (two species of spiny lobsters) were attracted to shelters emitting conspecific aggregation olfactory cues. There are numerous reasons why individuals would choose to shelter gregariously, for example improved access to mates and an increased ability to deter intruders. However, it is likely that the primary benefit is a reduction in predation levels via a dilution effect (Horner et al. 2006).

Another hypothesis for an individual choosing to shelter alongside conspecifics is that individuals may use the occurrence of an already present individual as an indicator of

the quality of a general habitat or specific refuge. A settled individual can therefore be used as a source of public information, where it may indicate a resource of higher quality (Danchin et al. 1998; Wagner and Danchin 2003; Donahue 2006). Minimally, the presence of another individual provides an indication that this is a location in which shelter is possible, and perhaps that this location is well suited to providing refuge. The observing animal can infer that if the shelter were low quality, the sheltering animal would likely have moved on.

Public information use is the collection of information about the relative quality of a resource by monitoring the success or failure of others (Valone 1989). Public information use therefore differs from local enhancement in that it provides information about the quality of an environmental resource, rather than where to find it (Valone and Templeton 2002). The ability to use public information can give individuals a distinct advantage, as they are able to gather information regarding the quality of a resource without having to incur the costs of sampling it for themselves (Coolen et al. 2003).

Habitat selection has been shown to be influenced by public information use in a range of taxa with regards to breeding site selection. Deutsch and Nedft (1992) conducted a study on choice of mating territory in two species of lekking antelopes, *Kobus kob Thomasi* (Uganda kob) and *K. leche kafuensis* (Kafue lechwe). By experimentally transplanting soil from successful mating territories to less successful ones, Deutsch and Nedft (1992) were able to manipulate the number of successful matings at each territory, with the previously less successful sites in both species receiving approximately 10 times the number of matings than prior to soil transplantation. Deutsch and Nedft (1992) explain this significant difference due to the transplanting of olfactory cues in the urine of females being transplanted to the less successful sites

alongside the soil. These olfactory cues are subsequently used by prospecting females to determine the quality of the mating site and/or male holding the territory, by receiving an indication of the number of females selecting that territory previously.

Public information use in the context of habitat choice for reproduction has also been shown in birds. Danchin et al. (1998) conducted a 17 year long study on breeding colonies of *Rissa tridactyla* (black-legged kittiwakes), a cliff-nesting seabird. During the study Danchin et al. (1998) discovered that breeding pairs tended to base their choice of cliff on which to breed on the success of the previous years' breeders. Failed breeders from a patch in which individuals had generally high patch-wide reproductive success tended to re-nest in the same patch the next year, whereas failed breeders from a patch in which individuals had low patch-wide reproductive success tended to nest in a different patch the next year. The decision of whether or not to switch cliffs was therefore not shown to be dependent on the personal success of the previous year, but rather the success of conspecifics and overall breeding success in each location.

Doligez et al. (2002) also showed public information use playing a role in habitat selection for breeding purposes in *Ficedula albicollis* (collared flycatchers), a small migratory passerine bird. Doligez et al (2002) manipulated two components of public information, the mean number of offspring raised locally ("quantity") and their condition ("quality") in a 2 year experiment on the island of Gotland, Sweden, by transferring 7-day-old nestlings between nests among breeding plots. This created plots where the mean number of fledglings per breeding pair was increased, decreased, or left unchanged. Fledgling quality was altered as a result of manipulation of quantity, with larger broods having fledglings with a lower body condition due to the increase in demand for food across the clutch. Immigration rate was shown to decrease with local

offspring quantity, but did not depend on local offspring quality, suggesting that immigrants are deprived of information regarding local quality. However, emigration rate was shown to increase both when local offspring quantity or quality decreased, suggesting that collared flycatchers already resident within a breeding plot are capable of using both components of public information (Doligez et al. 2002).

Public information use has been studied most extensively in a foraging context across a range of taxa (Templeton and Giraldeau 1995; Smith et al. 1999; Coolen et al. 2003; 2005; Kendal et al. 2009). For example, Templeton and Giraldeau (1995) carried out field trials using group-foraging European starlings in which the birds were presented with an artificial food patch differing in availability of public information. By raising the height of opaque barriers between sampling patches, it became difficult for the starlings simultaneously to collect both private information about their current chosen sampling patch through their own success and public information about other sampling patches through the observation of others' success. However, when these opaque barriers were low, it became possible to collect both types of information at the same time. The starlings were found to vary their use of public information in accordance to the sampling conditions they were presented with, choosing to use a combination of both private and public information to select the most profitable sampling patch when both were available simultaneously. However, relying solely on private sampling information when private and public information could not be gathered simultaneously and a choice had to be made between which type of information to collect. A similar experiment was also carried out by Smith et al. (1999) in *Loxia curvirostra* (red crossbills). The results of their experiment showed that red crossbills spent significantly less time sampling an empty foraging patch in the presence of two other conspecifics

than they did when sampling alone, suggesting that they were able to observe the success or failure of others foraging and switch patches accordingly.

Extensive studies have also been carried out studying the use of public information in fish. There have been several recent publications by Coolen et al. (2003, 2005) demonstrating the use of public information in a foraging context by ninespined sticklebacks as discussed in section 2.6.1.

Using the same experimental assay, Kendal et al. (2009) found that ninespined sticklebacks are also capable of deploying a 'hill-climbing' strategy when exploiting public information. Individuals with prior experience of foraging more successfully at one prey patch over another were shown to switch to the alternate patch when the prey capture rate of demonstrators was greater than that at the patch they had previously perceived to be the richer. Conversely, they were significantly less likely to switch to the alternative patch if the prey capture rate of the demonstrators was lower than that of the 'rich' patch based on their previous private information. Such a strategy, if widely deployed, potentially allows individuals in a population to steadily increase their foraging efficiency by gradually homing in on the most profitable foraging locations (Webster and Laland 2012).

Despite not utilising public information, threespined sticklebacks have been shown to employ the simpler social learning process of 'delayed local enhancement', whereby an individual is attracted to a location where others had previously been observed. Coolen et al. (2003) showed that both threespined and ninespined stickleback observers were able to use previously observed foraging cues of conspecifics to determine which of two prey patches contained food, despite the absence of food and demonstrators at the time of choice (Coolen et al. 2003).

Delayed local enhancement has also been shown in fishes under the context of cooperation. Bshary and Grutter (2006) designed a series of experiments using *Labroides dimidiatus* (a species of cleaner fish). These cleaner fish may cooperate by removing ectoparasites from clients, or they may cheat by feeding on client mucus, which they typically prefer over ectoparasites (Grutter & Bshary 2003). Bshary and Grutter (2006) allowed a client fish to view two cleaner fish and their corresponding model clients simultaneously. One was cooperating with the model as though it was feeding on ectoparasites, and the other was not interacting with a model client at all. The focal client fish was observed to spend a significantly higher proportion of time in close proximity to the cooperative cleaner fish than the uncooperative cleaner fish.

It is widely acknowledged that many fish species are attracted to structure within the environment and will move toward it. Such structure can include artificial reefs, vegetation, and floating algae (Holbrook and Schmitt, 1984; Walsh, 1985; Jara and Cespedes, 1994; Basset, 1994; West et al., 1994; Laegdsgaard & Johnson 2001) and can be used as a shelter for protection from predators. Shelters may differ in their quality reflecting variation in size (Hixon and Beets 1989) and location with regards to proximity to other resources, such as foraging patches. It is therefore likely to be beneficial to an individual to assess the quality of possible available shelters, an assessment for which the information provided by others might be of value.

As described above, public information use has been recorded in a variety of species and taxa under a range of different contexts. However, to the author's knowledge, to date there has been no assessment of public information use in any taxa under the context of refuge or shelter choice, a key resource for any prey species and worthy of attention. Here I assess the ability of both threespined and ninespined sticklebacks to

use the more simple social learning process of delayed local enhancement to select one of two identical shelters based on the previously observed presence or absence of conspecifics. In line with the experiments of Coolen et al (2003), assuming that these psychological abilities generalise across contexts, it would be logical to predict that both species would be able to employ the simple process of delayed local enhancement to select the previously occupied shelter.

3.2 Methods

3.2.1 Subjects and apparatus

Twenty ninespined sticklebacks and 20 threespined sticklebacks captured in Melton Brook, Leicestershire, UK (GRID REF: SP 602075) in April 2012 served as subjects. A further 80 of each species were used as demonstrators. In the laboratory, the fish were held in conspecific groups of 40 to 50 in 90L aquaria. Each aquarium contained a layer of coarse sand, an external filter, and artificial vegetation for cover. Overhead fluorescent lighting illuminated the holding tanks for 14 hr/day and the temperature was maintained at 8 °C. They were fed daily with frozen bloodworms (*Chironomid sp.*).

The experiment was conducted between July and September 2012 and excluded any individuals that displayed nuptial colouring or gravidity, as ninespined sticklebacks' use of public information is correlated with their reproductive state (Webster & Laland, 2011).

The experimental apparatus consisted of a glass tank (measuring 122cm by 30cm) filled with water to a depth of 20cm, and divided into three equal sections by two black lines at right angles to the tank's major axis, and visible through its glass floor. Two identical

artificial shelters (15cm by 15cm with a height of 22cm), covered from above with thick black plastic cut to size and constructed of a white mesh, that allowed passage of both visual and olfactory cues, were placed at opposite ends of each experimental tank. Each shelter, floored with coarse sand, contained an artificial plant. The remainder of the experimental tank, placed on white surface was bare to enhance the relative attractiveness to focal subjects of the shelters as places of refuge. A transparent circular holding compartment with a diameter of 10cm and a height of 25cm was placed in the centre of the tank (see Figure 3.1) A Canon HG20 video camera placed 1.2m above the tank permitted observation of the animals and video recording of their behaviour for later analysis.
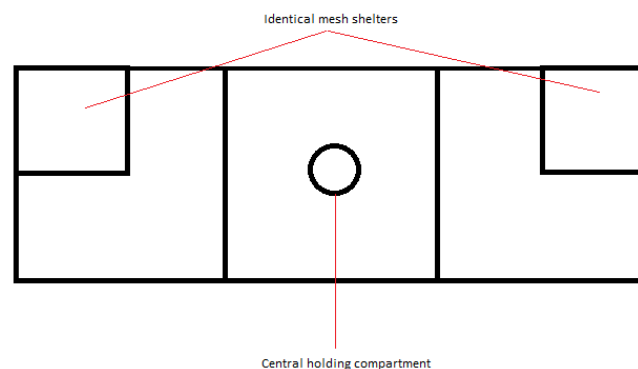
Figure 3.1: A plan view of the experimental setup.

3.2.2 Procedure

3.2.2.1 Demonstration phase

Four demonstrators, who were size matched conspecifics of each focal individual and unfamiliar to the subject, were placed in a randomly selected shelter and allowed to settle for 15min. After this time, the focal fish was placed in the holding compartment in the centre of the tank and allowed to settle for 10 min. At the end of the settling period, the holding compartment was removed and the focal fish was allowed to explore

the entire tank except for the inside the two shelters, one of which contained the demonstrators. The focal individual explored the tank for 30 mins and was then recaptured and temporarily removed from the experimental tank.

3.2.2.2 Test phase

While the focal fish was absent from the experimental tank, the demonstrators were removed from the shelter, then both shelters were removed from the tank, and the water within the tank was mixed for 30 sec to ensure that any residual odour cues from the demonstrators within the shelter were dispersed throughout the tank. The shelters were then replaced with two identical shelters, however, this time with a small entrance (3cm x 3cm) in the bottom centre of the front wall to allow access to both shelters.

The focal fish was returned to the holding compartment in the centre of the experimental tank and allowed to settle for a further 10 min, after which the holding compartment was removed and the focal fish was once again allowed to explore the tank, this time for a period of 20 min.

3.2.2.3 Video playback

The proportion of time that the focal fish spent in the third of the tank containing each shelter during both the last 20 min of the demonstration phase (to exclude initial exploratory behaviour) and the entire test phase was recorded. The proportion of time spent within each shelter during the test phase, the first line crossed, the latency with which each focal fish first crossed a line, and the first shelter entered by the focal fish was also recorded.

If the focal fish used the social learning process of delayed local enhancement in selecting a shelter, it could be predicted that the focal fish of both species would spend a significantly higher proportion of time in the vicinity of the shelter housing the demonstrators during the demonstration phase, a higher proportion of time inside the demonstrated shelter itself, and would select the demonstrated end of the tank and shelter first in a binary choice assay.

3.3 Results

3.3.1 Demonstration phase

Both the threespined sticklebacks and ninespined sticklebacks spent a significantly higher proportion of time in the vicinity of the shelter in which the demonstrators were housed during the demonstration phase of the experiment. Due to a high proportion of zeros within the data, it could not be normalised and a parametric analysis could not be used (Wilcoxon Signed Ranks Test: $Z_{18,1}$ = -2.113, P = 0.035 and $Z_{19,1}$ = -2.133, P = 0.033 respectively) (Figure 3.2). I can therefore be confident that the focal fish of both species were aware of the presence of the demonstrator shoal within the shelter. There was no significant difference observed in the proportion of time spent in the demonstrated end of the tank between the two species (Student's T-test: T = -0.674, df = 34, P = 0.505).
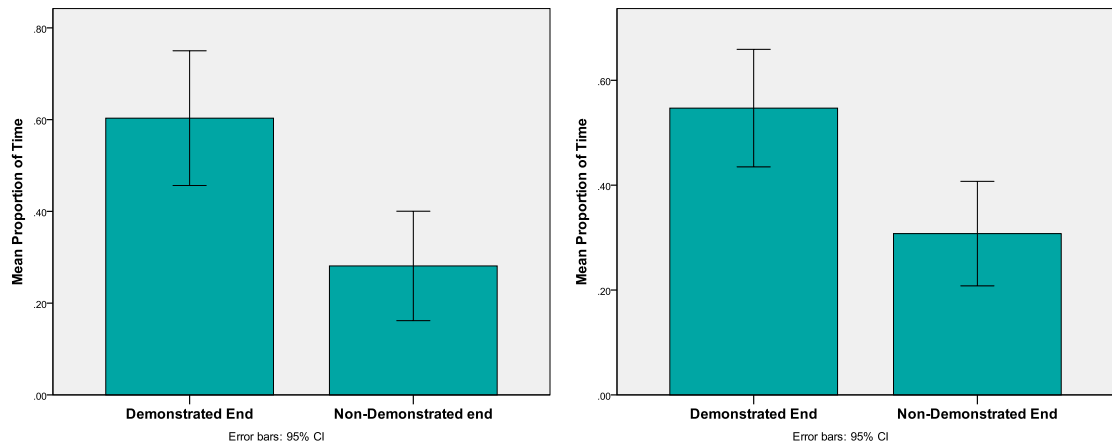
Figure 3.2: The mean proportion of time focal individuals spent in the demonstrated and non-demonstrated ends of the tank during the demonstration phase of the experiment. Left; threespined sticklebacks, Right; ninespined sticklebacks.

3.3.2 Test phase

However, neither the threespined nor the ninespined sticklebacks showed any significant difference in the proportion of time they spent in either the demonstrated or non-demonstrated ends of the tank during the test phase (inclusive of the time spent inside either shelter) (GLM: F = 0.606, df = 4, P = 0.661). Although from figure 3.3, it is visible that there was a slight trend toward the non-demonstrated end, this result is not a significant one and cannot be ruled out as having occurred by chance. There was also no preference for one particular end of the tank (left or right) (GLM: F = 0.001, df = 1, P = 0.974) and no significant difference observed in the proportion of time spent in the demonstrated end between the two species GLM: F = 0.432, df = 1, P = 0.515).
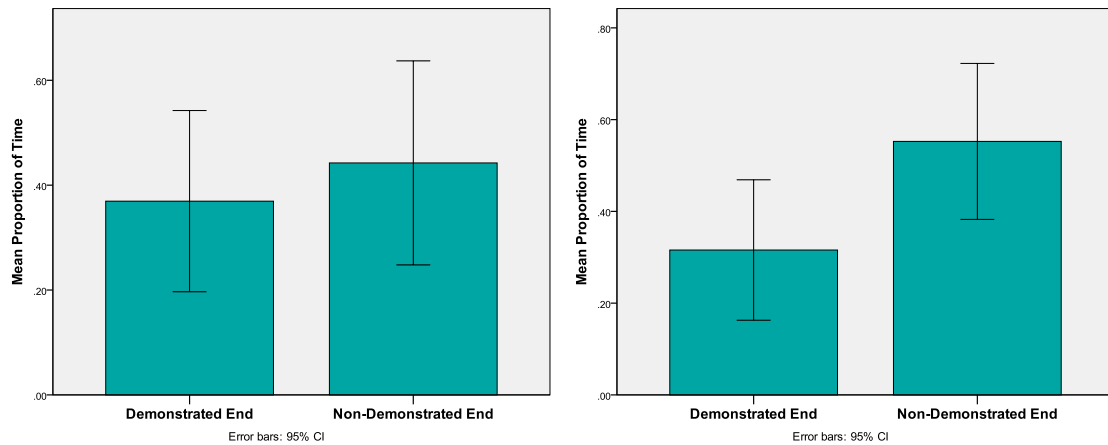
Figure 3.3: The mean proportion of time focal individuals spent in either the demonstrated or non-demonstrated end thirds of the tank, inclusive of the time spent in either shelter. Left; threespined sticklebacks, Right; ninespined sticklebacks.

3.3.2.1 Test phase binary choice

There was also no significant difference in either species between which shelter was entered first in a binary choice assay (either the demonstrated or non-demonstrated). It should be noted that not all focal individuals entered either shelter, with 11 threespines selecting a shelter and 19 ninespines (Binomial Test: N = 11, P = 1, N = 19, P = 0.359 respectively).

There was no significant difference discovered in the binary choice of the end of the tank first entered (demonstrated vs non-demonstrated) during the test phase in the threespines (Binomial Test: N = 18, P = 0.815). However, there was a significant difference observed in the binary choice of the end of the tank first entered (demonstrated vs non-demonstrated) during the test phase in the ninespines (Binomial Test: N = 20, P = 0.041), with 5 individuals choosing to enter the vicinity of the demonstrated shelter first and 15 individuals choosing to enter the vicinity of the non-demonstrated shelter first.

There was no significant difference between the two species when comparing the mean latency for which it took individuals during the test phase to enter either of the two end thirds of the tank (GLM: F = 0.823, df = 1, P = 0.370) (Figure 3.4). Although from Figure 3.4, it is visible that there was a slight trend for the ninespined sticklebacks to have a longer latency than the threespined sticklebacks, this result is not a significant one and cannot be ruled out as having occurred by chance.
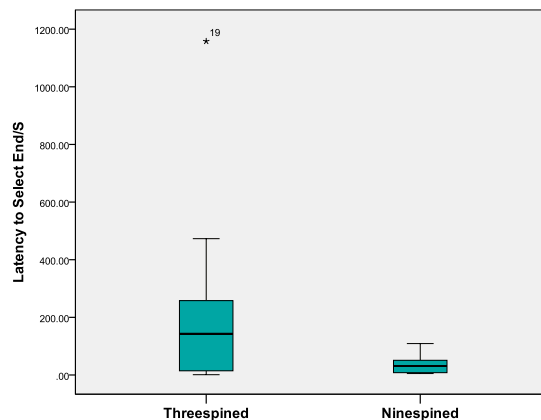
Figure 3.4: The latency of each species to leave the central third of the tank after being released from the holding compartment and enter the vicinity of either shelter during the test phase.

3.4 Discussion

Both threespined and ninespined sticklebacks were tested on their ability to use the social learning mechanism of delayed local enhancement to select a shelter previously inhabited by conspecifics by presenting them with two identical shelters, one of which containing a small shoal of conspecifics, and allowing them access to these shelters once the demonstrator shoal had been removed.

Both the threespined and ninespined sticklebacks spent a significantly larger proportion of time within the vicinity of the demonstrated shelter than the non-demonstrated shelter

during the demonstration phase (Figure 3.2). It can therefore be concluded that the focal individuals were aware of the presence of the demonstrator shoal within the selected shelter and that both species were attracted to the vicinity of the shelter in which the demonstrator shoal was housed. The thin mesh used to form the walls of the shelters meant that this attraction will likely have been through a combination of both visual and olfactory cues.

Neither ninespined nor threespined sticklebacks used delayed local enhancement to select the end of the tank in which they had previously observed conspecifics within a shelter during the test phase. Surprisingly, the ninespined sticklebacks selected the non-demonstrated end third of the tank first, however there was no overall difference in the proportion of time either species spent in each end section (Figure 3.3).

One possible explanation for the seemingly lack of preference between the demonstrated and non-demonstrated ends with regards to the proportion of time both species spent either within a shelter or within the vicinity of a shelter is that of stimulus enhancement. Stimulus enhancement occurs when the presence of a demonstrator in close proximity to, or interacting with, a stimulus in the environment (rather than a discrete spatial location) causes the observer to subsequently become more likely to interact with similar stimuli (Webster and Laland 2012). Generalisation is a crucial component of stimulus enhancement (Webster and Laland 2012) and can be used as a possible explanation for the findings of this experiment, whereby the observer becomes more likely to interact with, or be attracted to a similar stimulus in other locations (Hoppitt & Laland, 2008), rather than the specific stimulus in the specific location in which the demonstrator was observed. Therefore rather than using delayed local enhancement to select a shelter, both ninespined and threespined sticklebacks may be using generalised stimulus enhancement, whereby it does not matter which shelter is

selected, as they are both identical and are of a similar nature to the one in which the demonstrator shoal was observed and location does not play a role in shelter selection. Using non-identical shelters (e.g. different colours) would help to determine whether or not this is the case.

Another possibility is that the focal fish was unable to differentiate between the two shelters once having been reintroduced at the beginning of the test phase due to an absence of any spatial cues. It would be interesting to repeat the experiment with different coloured cues (e.g. spots) on or near each shelter.

When looking at the results as a binary choice test, neither the threespined sticklebacks nor the ninespined sticklebacks showed a significant preference for selecting either the demonstrated or non-demonstrated shelter first. These results are consistent with those found when looking at the proportion of time spent both within the demonstrated or non-demonstrated ends of the tank and suggest that neither species are using delayed local enhancement to influence their choice of shelter. However, when looking at a binary choice of the first end third of the tank to be chosen, the ninespined sticklebacks do show a significant preference for one over the other.

One possibility for this result is that the focal ninespines developed a negative association with the demonstrated shelter due to an observable negative effect coming from the demonstrators through behavioural cues. It may be that 15 minutes was not a long enough settling period for the demonstrator shoal and they were still stressed from handling. However, a 15 minute or less settling period has previously been used in a multiple number of behavioural experiments on sticklebacks with no noticeable negative effect (e.g. Coolen et al. 2003, 2005; Webster et al. 2008; Kendal et al. 2009) so it is unlikely to be the case.

Another possible explanation comes from three studies on social learning with rhesus macaques (Darby & Riopelle 1959), starlings (Templeton 1998), and more recently *Sciurus carolinensis* (Grey squirrels) (Hopewell et al. 2010). In these studies, a conspecific demonstrator opened one of two food containers, which was either empty or contained a food reward. Test subjects then had to select the same container if the demonstrator had found food and the opposite one if they had been unsuccessful. In all three studies it was found that the test subjects learned to select the opposite container to the empty one chosen by the conspecific more readily than to select the same one. This suggests that subjects were readily able to learn that the observation of a conspecific removing food from a specific location meant that food was no longer available. This phenomenon was termed 'the depletion effect' by Templeton (1998). Although these studies were all under a foraging context, the same principles as the depletion effect could apply to this current study under the context of shelter choice, but instead of the resource that is being depleted being food, it is space. When the ninespined sticklebacks observed the conspecific shoal residing in one shelter, that shelter may then have been regarded as full, encouraging the focal fish to then swim toward the alternative, empty shelter first on test. Support of this hypothesis can be found in a study by Holbrook and Schmitt (2002) on *Dascyllus flavicaudus* and *D. Trimaculatus,* two species of tropical damselfishes. They showed that individuals were most at risk from predation when located near or just outside the perimeter of a shelter and that predation risk also increased with population density due to intraspecific interactions among sheltering fish jostling for space in the safest regions; this resulted in the displacement of less aggressive individuals to riskier locations from whence they were predated upon.

Another hypothesis for the ninespined sticklebacks' avoidance of the demonstrated shelter under a binary choice test is that the fish perceived an empty shelter that was a

recent previous refuge area for conspecifics as an area of high predation risk, or unsuitable as a refuge by some other means, as the fish that had previously inhabited the shelter had moved on.

There was no significant difference between species in the latency to leave the central area and move into the vicinity of either shelter, however, as seen in Figure 3.6, there was a trend for the threespined sticklebacks to take longer than ninespined sticklebacks. Coolen et al. (2003) explained the species difference observed between threespines and ninespines in their ability to utilise public information, with ninespines able to use public information under a foraging context, whilst threespines could not, by a difference in their possession of anti-predator defences. Threespines have better protection from predators due to larger spines and the presence of an armoured pelvic girdle and plates (FitzGerald & Wootton 1996). This potentially allows them cope with increased exposure to predators and rely more on private information with increased sampling times but more accurate and current information. This private versus public information could also extend to a shelter choice context, with threespines affording to take longer to explore the open, central area of the environment than the ninespines therefore extending the latency with which they move into the vicinity of one of the shelters.

3.5 Summary

Neither threespined sticklebacks nor ninespined sticklebacks used delayed local enhancement to select a shelter they had previously observed to be inhabited by a small shoal of conspecifics, despite both species having previously been shown to be able to use this social learning mechanism in a foraging context. As a result of these findings, there was no need to alter the ratio of demonstrators in each shelter (and therefore vary

shelter quality) to extend the species comparison in a shelter choice context to test for public information use.

Chapter 4 now goes on to look at the use of another mechanism of social learning in threespined sticklebacks, the social enhancement of food preferences. This time under a foraging context.

Chapter 4. The social enhancement of food preferences

4.1 Introduction

Generalist foragers may often be faced with the opportunity to exploit several different food types at a single point in time and must be able to choose between them in order to forage efficiently. Individuals that live in groups have the advantage of being able to use social information through observation of the actions, choices and success rates of their groupmates. The use of social information potentially allows foraging animals to learn about the distribution and availability of different food types within their local environment without having to incur the costs associated with sampling the area for themselves (Kendal et al. 2009). This social information can either be acquired directly by observing the real-time actions of their groupmates, or it can be acquired indirectly using food derived cues, such as residual odour or the metabolic by-products of ingested food (Galef and Wigmore 1983; Galef 1988). This indirect form of social learning about food has been termed the social enhancement of food preferences (Hoppitt & Laland 2008) and has a distinct advantage to the observer in that it does not require the learner to be present while the demonstrator is exploiting the food resource.

Most of the studies into this form of social learning have focused on rodents and most extensively in the Norway rat (Galef et al. 1983; Galef & Wigmore 1983; Galef 1988; Galef 2005). Other studies include *Meriones unguiculatus* (Mongolian gerbils) (Valsecchi et al. 1996), and *Mesocricetus auratus* and *Phodopus campbelli,* two species of hamster (Lupfer et al. 2003). Galef and Wigmore first demonstrated the social enhancement of food preferences in adult Norway rats in 1983. They found that a naive rat (henceforth the 'observer'), after interacting with a recently fed conspecific (a 'demonstrator'), when given a choice between two novel foods, would preferentially

consume the same food type as the demonstrator. Galef et al. (1988) were able to determine that it is the presence of carbon disulphide on the breath of the demonstrator rats which is the key to observer rats developing a preference for a demonstrated food type. Observers exposed to a demonstrator that had recently consumed a cinnamon flavoured diet and observers exposed to a piece of cotton wool powdered with cinnamon and in addition, moistened with CS_2, both subsequently showed significant preferences for cinnamon flavoured food. In comparison, rats exposed to cinnamon powdered cotton wool moistened with distilled water did not develop a preference for cinnamon (Galef et al. 1988). Munger et al. (2010) identified a specialised olfactory subsystem that is sensitive to carbon disulphide and required for the acquisition of socially transmitted food preferences in mice. Disruption of this olfactory subsystem resulted in a failure to acquire socially transmitted food preferences (Munger et al. 2010).

The social enhancement of food preferences has also been documented in other social mammals, including *Carollia perspicillata* (the short-tailed fruit bat) (Ratcliffe & ter Hofstede 2005), and *Canis familiaris* (the domestic dog) (Lupfer-Johnson & Ross 2007). Ratcliffe & ter Hofstede (2005) presented demonstrator bats with either cinnamon or cocoa flavoured food. Demonstrators were then placed into the cage of a single observer and allowed to interact for a period of 30 mins. After this interaction, all observers displayed a preference for the demonstrated diet when presented with both food types. Ratcliffe & ter Hofstede (2005) also discovered that short-tailed fruit bats readily reversed their food preference when later allowed to interact with demonstrators which had recently consumed the opposite flavour food to that which was previously demonstrated.

Lupfer-Johnson & Ross (2007) found similar results in dogs. Demonstrators were fed either basil- or thyme-flavoured food immediately prior to being allowed to interact with an observer for a period of 10 mins. The observer then displayed a significant preference for the same flavour food as had been consumed by the demonstrator.

The phenomenon of socially enhanced food preferences in Norway rats has been shown to have a strong influence on observers. Even observer rats that have been conditioned to show an aversion toward a particular food as a result of experiencing gastrointestinal distress immediately after consumption, were observed to reverse this previously learned negative response when presented with demonstrators that had eaten the same food (Galef 1986). This process exhibits several possible functions. One is that it serves to increase the repertoire of foods available to an individual. Consistent with this hypothesis, Galef (1993) noted that observer rats were more influenced in their food choices by demonstrator rats that ate an unfamiliar food than by those that ate a familiar one. Galef (1993) points out that if the social learning of food preferences were to have a greater influence on observer rats eating foods already familiar to them, it would increase the tendency for rats to limit their diets only to foods already in their repertoire. However, with observers being influenced more by demonstrated novel food, social interactions serve as a means to expand dietary repertoires (Galef 1993).

A second possible function is the indirect avoidance of unpalatable or poisoned food types. Direct evidence for the avoidance of foods has consistently been found not to be present in rats (Galef et al. 1983, Galef and Beck 1985, Galef et al. 1990). However, indirectly, rats may inadvertently avoid consumption of unpalatable or poisoned foods through traditions for consuming palatable alternatives.

Socially learned food avoidance has also been shown to be absent in *Macacca fuscata* (Japanese macaques) (reviewed by Visalberghi 1994). There is however, substantial evidence of the social transmission of the avoidance of foods in several avian species. For example, *Passer domesticus* (house sparrows) were observed to consume significantly less red coloured food after watching conspecifics consume red food treated with quinine, which gave the food a bitter taste (Fryday and Grieg-Smith 1994). Another example is *Agelaius phoeniceus* (red-winged blackbirds) avoiding food associated with conspecifics displaying toxin-induced illness (Mason and Reidinger 1982, 1983). Also domestic layer strain chicks avoided pecking beads of the same colour to which they had previously observed conspecifics display a disgust reaction due to them being coated in bitter tasting methyl anthranilate (Johnston et al. 1998).

Shoaling fishes have recently been shown to be able to detect prey-specific cues generated by foraging conspecifics, a process that resembles the social enhancement of dietary preferences described above. The arrangement of fish shoals tends to be affected by a variety of phenotypic factors, including size, species, and age class (Hoare et al. 2000). However, there are also more subtle factors that affect shoal structure, including specific individual recognition (Griffiths and Ward 2006) and resource-specific chemical cues (Webster et al. 2008a).

When making shoaling decisions, individual threespined sticklebacks have been repeatedly shown to shoal preferentially with others that have recently occupied the same micro-habitat as themselves (Ward et al. 2004(c), 2005, 2007; Webster et al. 2007, 2008a, 2008b). A variety of species including *Salvelinus alpinus* (Arctic char) (Olsen et al. 2003), guppies, (Morrell et al. 2007), and threespined sticklebacks (Ward et al. 2004(c), 2005, 2007; Webster et al. 2007, 2008a, 2008b) are also able to recognise and choose to shoal with others that have recently consumed the same prey type as

themselves. Ward et al. (2005) even observed recognition of the same prey type occurring between species. Threespined sticklebacks showed self-referent matching to both habitat and diet cues, not only to conspecifics but also to stimulus shoals of ninespined sticklebacks.

There are several hypotheses as to why a mechanism allowing fish to detect and identify food cues from others has evolved. Shoaling fishes potentially gain a number of benefits from shoaling with individuals with a preference to exploit the same resources as themselves (Webster et al. 2008a). Social foragers are known to benefit from higher rates of prey detection than those foraging on their own. By shoaling with and monitoring the success of conspecifics that are exploiting the same prey type as themselves, an individual may be able to gain information about the distribution of prey types others are exploiting. It is also reasonable to hypothesise that unfed fish might use this source of social information to match their own prey use patterns with prospective shoal mates. Hungry fish could also learn about prey types that are locally abundant, or that they have not previously encountered before, by indirectly monitoring the prey use of others.

In a study on the social enhancement of food preferences in threespined sticklebacks by Atton (2010), small demonstrator shoals were fed one of two novel food types and then placed in a tank with either a black or a white base for an hour alongside a single observer fish. In accordance with previous studies into the social enhancement of food preferences in other taxa, it would be logical to predict that observers would display a preference for the demonstrated food type. However, when conditioned with the demonstrator shoal on a black base, observers were shown to have no preference for either food type and when conditioned with the demonstrator shoal on a white base, the observers displayed a significant preference for the non-demonstrated food type.

Threespined sticklebacks are preyed upon by many species of piscivore, both fish and birds. The sticklebacks, like many other species of small fish possess countershading, a gradation in colour from dark on the dorsum to light on the ventrum (Ruxton et al. 2004). Countershading is considered an adaptive trait for protection against predators concealing shadows cast upon the body by overhead illumination (Ruxton et al. 2004). In fish, the dark dorsal side provides cryptic colouration from aerial predators whilst the lighter ventral side provides camouflage from predators beneath them in the water. Threespined sticklebacks are therefore highly visible to avian predators when placed in tanks with a white base, as the darker dorsal side of the fish contrasts strongly with the substrate. Threespined sticklebacks avoid areas of white, most likely for this very reason, and being confined in a tank with a white base may be stressful for them.

Atton (2010) therefore attributed the observed aversion to the demonstrated food to a negative association developed by the observer due to stress. However, it is also possible that the negative association was formed due to indirect cues of stress emitted by demonstrators. This current study follows on from Atton (2010) and aims to clarify the mechanism behind the observed aversion to the demonstrated food when conditioning occurred on a white base.

Food-derived amino acids in urine provide a possible medium for transmission of food-specific cues. The epidermal mucus coating of fish provides another. Both have been shown to be used by fish in individual recognition. For example, by manipulating the diet of *Ictalurus nebulosus* (bullhead catfish), Bryant and Atema (1987) were able to change the behaviour patterns exhibited toward conspecifics, demonstrating that the food-derived amino acids in urine are used in individual recognition. Matsumura (2004, 2007) showed that epidermal mucus contains phosphatidylcholines which, like the food-derived amino acids, are also involved in individual recognition and may have an effect

62

upon diet choice (Matsumura 2007). Both of these possible mechanisms require further investigation to determine whether either, or both, of them play any role in the social transmission of food preferences, or avoidance as seen in this case.

By changing the base colour of the tank before introducing the observer, I hope to be able to distinguish whether the negative association seen previously by Atton (2010) is as a result of the observers receiving the food cues simultaneously to being in a stressful situation, or as a result of the demonstrators giving indirect cues to the observer of both food type and stress cues through the water. If the latter is the case, I should also receive some indication as to the mechanism by which these cues are transferred.

If the first hypothesis is correct; that a negative association is formed due to stress upon the observer when simultaneously receiving food cues from a demonstrator, it is likely that there would be no preference for either food type, or a positive preference for the demonstrated food type if the observers are not experiencing stressful conditions at the time of receiving the food cues, regardless of whether or not the demonstrators were under stress at the time of emitting them.

If however, the negative association to the demonstrated food type is formed due to the observer receiving indirect stress cues from the demonstrators through the water, a preference for the non-demonstrated food type would be observed when the demonstrators are under stress at the time of emitting the cues, regardless of whether or not the observers were under stress at the time of receiving them.

4.2 Methods

4.2.1 Design

The experimental procedure was split into 4 stages; feeding a demonstrator shoal, conditioning the demonstrator shoal, presenting the demonstrator shoal to an observer in

the same water in which the demonstrator shoal had been housed in stage 2, and finally

testing the observer for a food preference (see Figure 4.1). The dependant variable was

the food preference displayed by the observer in the final test phase, either the

demonstrated or the non-demonstrated food type. The independent variables were the

condition under which the demonstrators were housed in stage 2 (stressful or non-

stressful) and the condition in which the demonstrators were presented to the observer

in stage 3 (stressful or non-stressful but opposite to the condition used in stage 2).
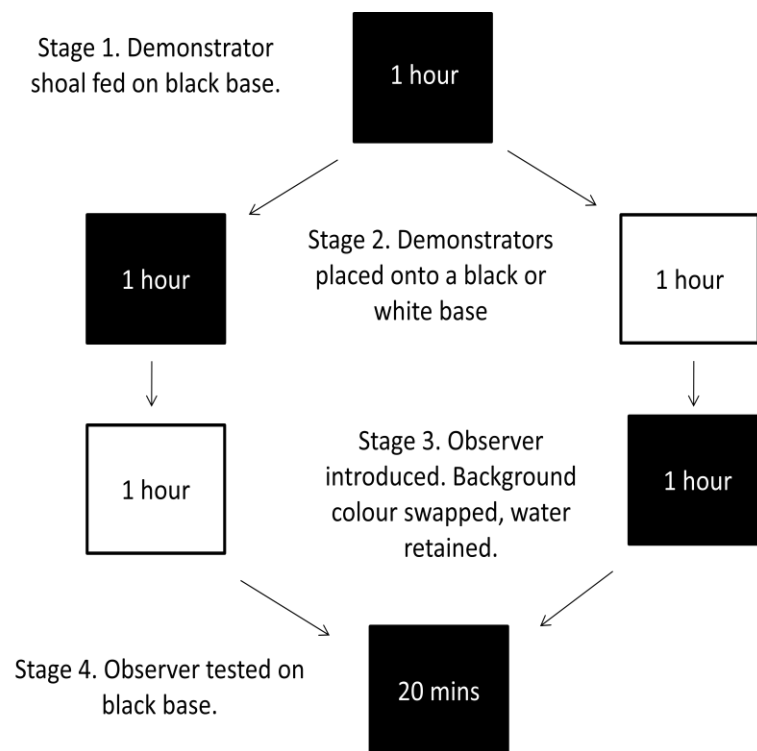
Figure 4.1. A flow diagram describing the different stages of the experimental
procedure.

4.2.2 Subjects

Threespined sticklebacks measuring circa 20mm were collected from the upper estuary

of the Kinnesburn, a small stream in Fife, Scotland, in January 2010. They were held in

the laboratory in groups of 15 fish in 30L aquaria, at 8°C under a 12 hour light / dark

cycle. The fish were fed adlib bloodworm daily. Experiments were carried out between

February and May 2010. No individuals were used that were displaying signs of illness, nuptial colouration, or gravidity and no individual was used in the experiment more than once. All fish were deprived of food for 24 hours prior to testing to ensure motivation to feed. Each trial used 4 demonstrator fish and 1 observer.

4.2.3 Apparatus

Stage 1 used glass tanks measuring 30 x 30 cm with a water depth of 20cm and no substrate. All vertical sides of the tanks were blacked out using black plastic wrapped around the outsides of the tanks to prevent outside disturbance. The tank was rested on a black surface. Two different prey types were used. These were frozen blocks of *Artemia spp.* and *Tubifex tubifex* (tubifex worms) chopped into 1mm pieces and allowed to defrost in water. Both foods were novel to both the demonstrators and the observers. *Artemia* naturally occur in hypersaline conditions, while tubifex are found in silty sediments in slow flowing or still water. The fish used in this study came from a fast flowing freshwater stream with a sand and gravel substrate and are therefore unlikely to have encountered these prey types previously.

The second and third stages used tanks measuring 30 x 30 cm with a water depth of 10cm. In the centre of each tank in stage 3 was a circular holding compartment measuring 5cm in diameter and 15cm in height through which both visual and olfactory cues could be transferred. Half of the tanks were placed on a white surface and half were placed on a black surface. All vertical sides were shielded from outside disturbance with black plastic.

Stage 4 of the experiment was the test tank, measuring 30 x 30 cm with a water depth of 10cm. Two petri dishes measuring 10cm in diameter containing the two food types (artemia and tubifex) were placed on opposite sides of the tank. There was also a

cylindrical holding compartment in the centre of the tank measuring 5cm in diameter and 15cm in height through which the focal fish could detect both visual and olfactory cues from the two prey types. The test tank had a black base to minimise stress.

4.2.4 Procedure

4.2.4.1 Stage 1

Shoals of four demonstrator fish, size matched to within 2mm in length, were placed into the first tank and allowed to settle for 15 min, after which an excess of either tubifex or artemia was added to the water, ensuring that all demonstrator fish had the opportunity to feed. The demonstrators were allowed to feed for 1h. during which time all were observed to feed. In all cases food items remained at the end of this hour suggestive of satiation. 13 trials used tubifex as the demonstrated food type and 12 trials used artemia.

4.2.4.2 Stage 2

The demonstrators were then placed into the second tank with either a black or white base and were left for 1h. Care was taken to ensure that no remaining food items were transferred with the demonstrators from stage 1 to stage 2.

4.2.4.3 Stage 3

Both the demonstrator shoal and the water in which they were housed during stage 2 were then transferred to the tanks used for stage 3. If the demonstrators had been housed on a black base in stage 2, they were transferred to a tank with a white base in stage 3 and vice versa. The demonstrators had therefore been moved either: (1) from a stressful situation to a non-stressful situation or (2) from a non-stressful situation to a stressful one. The water in these tanks therefore contained stress cues (i.e.cortisol) plus food cues if they had been moved from white to black, or food cues only if they had been moved

from black to white. Demonstrator shoals were allowed to settle for 15 minutes, after which a focal fish (size matched to within 2mm of the demonstrator shoal) was placed in the central holding compartment. All five fish were left for a further hour after which the demonstrator shoal was removed.

4.2.4.4 Stage 4

15ml of both food types were added separately into the two petri dishes in the test tank using a pipette. Care was taken to ensure that no food items moved outside of the petri dishes and any food items that floated were removed with a net. The focal fish was then placed in the central holding compartment of the test tank and allowed to settle for 10 minutes. After this time the focal fish was released and allowed to feed from the two petri dishes containing the two different food types (artemia and tubifex), one of which was previously eaten by the demonstrator shoal. The position of the two foods within the test tank was counterbalanced across trials.

Trials were filmed using as Canon HG20 video camera placed 1.5m in front of the test tank. From each trial I recorded the first food type that was selected and the number of food items of each food type that were consumed within a 2 minute period directly following the first selection. If neither food type was consumed after 20 minutes, the trial was abandoned. 3 trials were abandoned in the black to white condition and 7 trials were abandoned in the white to black condition. I also recorded the latency with which each observer began to feed.

4.3 Results

4.3.1 Non-stressful to stressful (black to white)

After focal fish interacted with demonstrators on a white background in stage 3, where the demonstrators had been housed with a black background in stage 2, they displayed

67

no significant preference for either the demonstrated or non-demonstrated food type during the test phase. This was observed in the first food item they selected, with 6 individuals consuming the demonstrated food type first and 7 individuals consuming the non-demonstrated food type first (Chi squared: $\chi^2 = 0.077$, $n = 13$, $P = 0.782$) (Figure 4.2 (left)). There was also no significant preference observed for either food type in the total number of food items consumed within the 2 minutes directly following their first selection (Wilcoxon Signed Ranks Test: $Z_{12,1} = -0.268$, $P = 0.789$) (Figure 4.3 (left)).
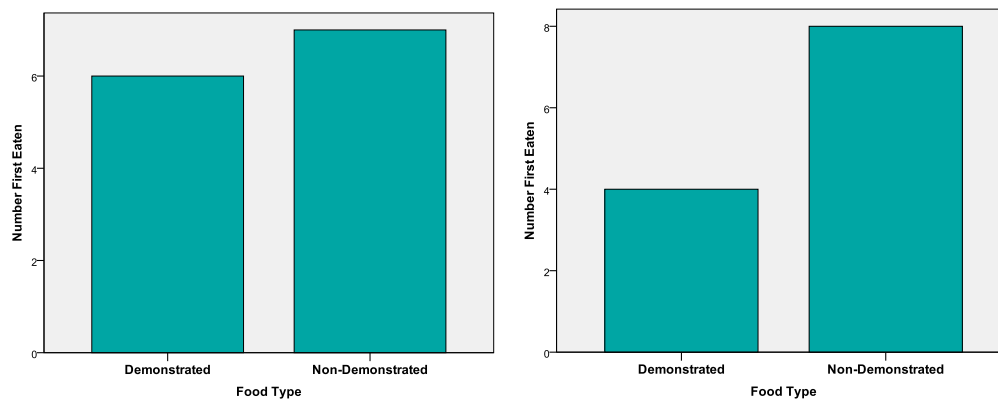
Figure 4.2: The number of times the demonstrated food and non-demonstrated food types were first to be consumed by the observers when the observers were conditioned with the demonstrators in tanks with a white base but which had previously been housed in tanks with a black base (left) and when the observers were conditioned with the demonstrators in tanks with a black base but which had previously been housed in tanks with a white base (right).
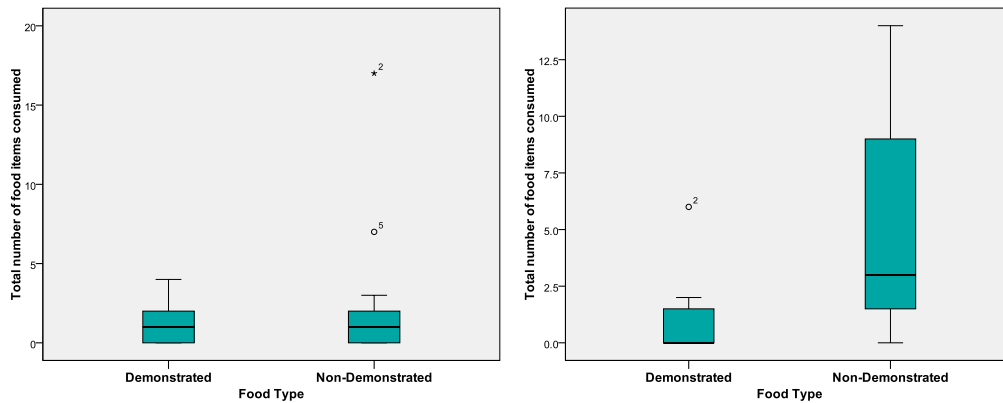
Figure 4.3: A boxplot showing the number of demonstrated and non-demonstrated food items consumed within 2 minutes after first selection when conditioned with demonstrators on a white base, which had previously been housed on a black base (left) and when conditioned with demonstrators on a black base, which had previously been housed on a white base (right).

4.3.2 Stressful to non-stressful (white base to black base)

Under this condition there were 12 successful trials and 7 abandoned trials. When observers were allowed to interact with demonstrators on a black background in stage 3, after the demonstrators had previously been housed in a tank with a white background in stage 2, observers again displayed no significant preference for either the demonstrated or non-demonstrated food type during the test phase in the first food item they selected, with 4 individuals consuming the demonstrated food type first and 8 individuals consuming the non-demonstrated food type first (Chi squared: $\chi^2 = 1.333$, $n = 12$, $P = 0.248$) (Figure 4.2 (right)). However, there was a significant preference observed for the non-demonstrated food type in the total number of food items consumed within the 2 minutes directly following their first selection (Wilcoxon Signed Ranks Test: $Z_{11,1} = -2.010$, $P = 0.044$) (Figure 4.3 (right)).

4.3.3 Comparisons between treatments

There was no significant difference between treatments in the number of times the focal fish consumed the demonstrated or non demonstrated food types first (2x2 Chi Squared:

$\chi^2 = 0.427$, *df* = 1, *P* = 0.404). However, there was a significant difference between treatments in the total number of both the demonstrated and non-demonstrated food types consumed (2x2 Chi Squared: $\chi^2 = 5.198$, *df* = 1, *P* = 0.020) with greater consumption of the non-demonstrated food by the observers in the 'white to black' treatment than in the 'black to white' treatment.

There was no significant difference between the two treatments in the latency with which the focal fish began feeding during the test phase (Mann Whitney: *U* = 53, n = 12,13, *P* = 0.186) (Figure 4.4).
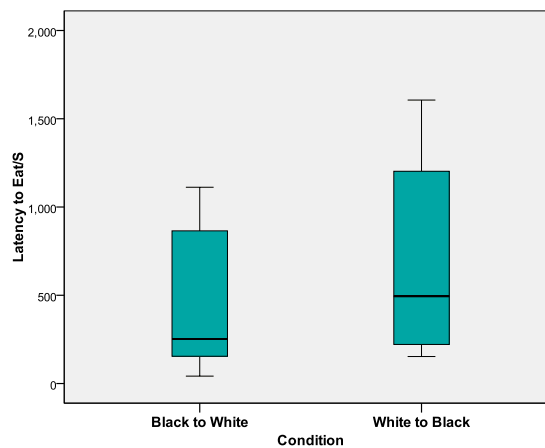
Figure 4.4: The latency with which the focal fish began feeding under each condition.

There was also no preference observed for either food type across both conditions, with the number of artemia and tubifex food items consumed being exactly equal at 36 each.

4.4 Discussion

Observer threespined sticklebacks were able to detect and identify prey-specific cues from shoals of conspecific demonstrators and use this information, not to enhance their selection of a demonstrated food, but to avoid a novel food type when prey-specific cues were received from demonstrators previously housed under stressful conditions.

Observers that interacted with demonstrators in a tank with a white base in stage 3 and a black base in stage 2 showed no preference for either the demonstrated or the non-demonstrated food type. However, observers that interacted with demonstrators in a tank with a black base in stage 3 and a white base in stage 2 showed a significant preference for the non-demonstrated food type. Taken together, these findings suggest that it is the stress of the demonstrators rather than of the observers that is critical for information transmission. Observers appear to form an aversion to food odour cues as a result of demonstrators simultaneously emitting cues indicating stress.

As seen in Figure 4.2, there was no significant preference shown for either food type when observers were allowed to interact with demonstrators in a tank with a white base in stage 3 when the demonstrators had been conditioned on a black base in stage 2. It can therefore be deduced that under these conditions, observers do not develop a negative association with the demonstrated food type, implying that they do not form an association between their own stress and the food cues received from the demonstrators. However, when observers were allowed to interact with demonstrators in a tank with a black base in stage 3 when the demonstrators had been conditioned on a white base in stage 2, a negative association with the demonstrated food type is formed, with the observers showing a significant preference for the non-demonstrated food type when looking at the total number of prey items consumed in each trial (Figure 4.3).

The primary response of teleost fishes to a stressful situation includes the rapid release into the circulation of the stress hormones catecholamines and cortisol (Ellis et al. 2004). Teleost fish are known to excrete cortisol into the water via the gills (Ellis et al. 2004). Consequently, it is possible that observers detect the cortisol together with food-derived amino acids excreted via the urine or epidermal mucus, giving rise to associative learning.

Individuals of a wide variety of species across taxa can be conditioned to avoid a certain food or property of a food by making the animal ill after consumption. This type of conditioning is often very effective with a marked aversion often being observed after just a single trial (Pearce 1997). It is also possible to condition animals to avoid certain foods through observations of conspecifics. The experiments of Fryday and Greig-Smith (1994) and Johnston et al. (1998), discussed in the introduction, show that birds are able to learn a negative association to a particular object or food characteristic by observing the disgust reactions of conspecifics to a bitter taste. A negative association can therefore be formed without the observer having to experience the negative effect themselves. It is highly plausible that negative associations to certain food types can also be formed in this manner in fish. If the stress cues of others take on negative secondary reinforcing properties as a result of past experience then they could act to inhibit diet consumption when associated with diet cues.

One hypothesis for the results in this experiment is that it is stress cues from the demonstrators alongside the prey-specific cues being excreted in the urine or epidermal mucus of the demonstrators that allow observers to develop a negative association to the demonstrated food. If it were the observers being stressed at the time of receiving the prey-specific cues from the demonstrators, it is likely that I would have seen a preference for the non-demonstrated food type in observers that interacted with demonstrators on a white base in stage 3.

I can also hypothesise that the mechanism behind the formation of the negative association is one of chemical cues from the demonstrator shoal, rather than behavioural cues. If the negative association in the observers were formed from behavioural stress cues received from the demonstrator, it is likely that I would have seen a preference for the non-demonstrated food when the observers interacted with demonstrators on a white

base in stage 3. However, a preference for the non-demonstrated food was developed when observers interacted with demonstrators on a black base, during which time the demonstrators (and observer) were not under stressful conditions and therefore should not have been displaying behavioural cues to the contrary. However, the water within the tank was taken from the hour in which the demonstrators were conditioned on a white base (in stage 2) and therefore under stress. Cortisol from this period of time, alongside the prey-specific cues were most likely still able to be detected in the water by the observers and as such, a negative association for the demonstrated food was formed.

However, these conclusions can only be drawn under the assumption that both the cortisol and the food cues need to be emitted simultaneously to elicit an effect. Further work needs to be undertaken to investigate this hypothesis and clarify the mechanism behind the results seen (i.e. by quantifying cortisol levels).

4.5 Summary

In sum, while there is extensive evidence amongst animals for the social transmission of information through which the observer and demonstrator come to exhibit the same behaviour, it is comparatively rare for animals to learn from conspecifics what not to do, leading observing animals to perform different, or opposite, behaviour from their demonstrators. However, in circumstances where demonstrator animals exhibit signs of stress, avoiding performance of their behaviour may be adaptive. Here I show that sticklebacks avoid the diet of stressed conspecifics. My findings thereby establish a novel mechanism for the avoidance of maladaptive information transmission in fishes. It is plausible that this mechanism may be widespread in teleost fishes.

The following 3 chapters examine the use of social networks in the study social learning, starting with Chapter 5, which introduces the concept of social networks and gives an overview of the merits of using social network analysis under a variety of contexts.

Chapter 5. An Introduction to Animal Social Networks

The following two data chapters, Chapters 6 and 7, examine how social learning may be influenced by the social network. The social network is an important feature of a population for a number of reasons and may influence the spread of novel behaviours. This chapter introduces the reader to the concept of social networks and the many uses of social network analysis.

5.1 What is a social network?

A network can be defined as a system of interacting components. The term is applied across all walks of life from anything from transport networks (Sen et al. 2003) to communication systems such as the internet (Tadic 2001). The study of network theory has been utilised widely by biologists and networks can be applied at a variety of biological levels (Krause et al. 2007). For instance, Barabasi and Oltavi (2004) were able to present insight into the functional organisation of the cell using gene and protein interaction networks; Laughlin and Sejnowski (2003) used neural networks to show how complex processes are controlled by interconnected cells; and Dunne et al. (2002) assessed how communities may be affected by invasive species by using the network of trophic interactions between organisms. The study of network theory is also used widely outside of biology (Newman 2010).

Considering the use of networks in the social aspects of biology, the social network structure of a group or population quantifies the pattern of interactions and relationships among its individuals (Hinde 1976; Whitehead 1997; Sih et al. 2009). A group's social network structure, and the specific network position of any individual within it, can have significant effects on social dynamics, individual fitness, and group function and

in turn can affect the evolution of social behaviour (Sih et al. 2009). The social network structure of human populations has been studied extensively by social scientists (Scott 2000), however, the study of social network structure in non-human animals, by comparison, has only recently received attention (Wey et al. 2007; Croft et al. 2008; Sih et al. 2009).

Studies on group-joining preferences have highlighted that individuals within a group or population commonly assort by phenotypic characteristics, which in turn is highly likely to generate a non-random network structure. Such phenotypic factors include sex (Reader & Laland 2000), familiarity (Swaney et al., 2001), size (Hoare et al., 2000), and hunger level (Krause, 1993). Indeed, there are several empirical studies that suggest that both captive and wild animal populations are characterised by a non-random social network structure (Croft et al., 2005). This has been seen in a variety of taxa, including fish (guppies) (Griffiths & Magurran 1997a; Croft et al. 2004), cetaceans (*Tursiops truncatus* (bottlenose dolphins) (Lusseau 2003), and birds (starlings) (Boogert et al., 2008).

A network can be visualised as a graph made up of edges and nodes, with nodes representing each individual within the network and edges representing any interaction (or association) between two nodes (Croft et al. 2004). Network theory provides a number of useful metrics for quantifying the social structure of a population. These include cluster analysis, path length analysis, and degree. Cluster analysis gives a measure of the mean clustering coefficient and can be classed as a local measure of cliqueishness (Croft et al., 2004). The clustering coefficient of a node (node A) is the fraction of pairs of individuals connected to node A that are also connected to each other. The average clustering coefficient of all nodes gives the global clustering

coefficient. A high global clustering coefficient is indicative of a heterogeneous network, rather than one arrived at by chance. There is evidence to suggest that a high clustering coefficient will decrease the spread of epidemics, as any infection would likely be contained among a small group of highly inter-connected individuals (Newman 2003). However, a high clustering coefficient may also inhibit the transmission of information through a population, depending on how tightly each cluster is maintained.

The path length (or geodesic) is the smallest number of connections (edges) by which one node can be reached from another (Croft et al., 2004). Taking the mean geodesic gives an indication of how closely interconnected the network is as a whole. This can also have an influence upon the spread of both disease and information through a population, with a low mean geodesic indicating a highly interconnected network and in turn the possibility for rapid transmission (Croft et al., 2004).

The degree of each node is calculated simply by taking the number of edges joined to it (Croft et al., 2004). If an individual has a high degree, it is probable that an innovation from that individual will be more likely to spread than if an innovator has a low degree (Croft et al., 2004).

5.2 Why study social networks?

The study of animal social networks has the potential to provide of us with a wealth of knowledge concerning the behaviour of animals under a wide variety of contexts that was previously inaccessible by other means.

5.2.1 Cooperation

There are a number of areas under the umbrella topic of animal behaviour where the study of social networks could provide valuable insight. One such area is the study of cooperation. Croft et al. (2006) conducted a study on the social network of populations of free-ranging Trinidadian guppies, in which repeated persistent interactions were recorded between pairs of females. Interestingly these repeated interactions were not found between pairs of males or between mixed sex pairs. On exposure to a predator, pairs of females that persistently interacted within the network were regularly observed together during bouts of predator inspection, whereby small groups will approach and assess a possible predator. Pairs of fish were then isolated in a further experiment during which it was recorded that pairs which had previously experienced frequent interactions with one another as part of the network were more cooperative in their predator inspection behaviour. This was apparent by the pairs switching the more dangerous lead position more often than pairs which had not experienced frequent interactions with one another. The social network therefore has the potential to be used as a good predictor of cooperative behaviour.

5.2.2 Disease transmission

Networks have frequently been used to investigate how disease transmission may be influenced by social interactions between individuals and populations (e.g. Watts and Strogatz 1998; Potterat et al. 2002; Cross et al. 2004; Corner et al. 2003). However, the majority of studies which use a network approach have focused on human populations, with very few studies having been conducted on animal populations to date (Krause et al. 2007). The social network of a population is an important consideration when looking at the spread of disease. It may be possible to predict the pathway of transmission and the speed at which transmission may occur. In some cases, it may also

be possible to identify individuals that have a large number of connections within the social network and could therefore be likely to increase the spread of disease significantly (Corner et al. 2003; Christley et al. 2005).

Integrating data from the social networks of animal populations with disease transmission dynamics has great potential for understanding and perhaps limiting the spread of disease. This is of great importance when considering an endangered species or the spread of disease through livestock. Using pair-wise association data of *Syncerus caffer* (African buffaloes) collected over two years, Cross et al. (2004) studied the potential for the spread of bovine tuberculosis. They integrated the empirical behavioural data with simulation models of disease spread, using the time spent in a herd with infected conspecifics as a predictor for the probability of becoming infected. It was discovered that non-random association patterns are an important factor in the spread of disease, particularly if the disease requires only a relatively short association period for transmission. Another study by Corner et al. (2003) used a networks approach to study the spread of bovine tuberculosis through a population of *Trichosurus vulpecula* (brushtail possums), an infector of livestock in New Zealand. In this case, they were able to use the behaviour of den sharing as a predictor as to the transmission of disease.

Similar to disease transmission, social networks may also be used to assess the transmission of parasites within and/or between populations. Godfrey et al. (2009) used the behaviour of sharing rock crevices to map the transmission of parasites between individual *Egernia stokesii* (gidgee skinks). Two lizards were classed as being

connected if they used the same crevice within an estimated transmission time for parasite infection.

As well as using the social network to predict the spread of a disease through populations, it may also be used on an individual level basis by predicting the likelihood of a particular individual to become infected (e.g. Christley et al. 2005). The probability of an individual becoming infected is likely to be determined by a variety of factors related to the social network, such as the number of network connections it has, the proportion of those individuals it is connected to that are infected, and the frequency of contact with those infected (Christley et al. 2005). There is huge potential to use such a method in the conservation of endangered species through identifying individuals with a high risk factor and ensuring measures are taken to minimise the risk of infection.

5.2.3 Social structure and identifying the role of individuals

Studying the social network of a population can also provide valuable insight into the importance of different social interactions and how the characteristics of individuals can affect social structure. For example, Flack et al. (2006) used knockout experiments on a captive population of *Macaca nemestrina* (pigtailed macaques) and were able to determine key individuals in the network with regards to policing behaviour. In the absence of these few individuals, the previously observed social network was destabilised, with group members forming smaller, less diverse, and less inter-connected networks.

Lusseau and Newman (2004), studying association data of bottlenose dolphins in New Zealand, identified communities and smaller sub-communities within the dolphin population, with sub-communities being more likely to contain members that are the

same sex and of a similar age. They also identified some key individuals, crucial to the maintenance of social cohesion of the population as a whole, by providing links between sub-communities.

Ramos-Fernández et al. (2009) carried out a long-term study on the association patterns of a group of wild *Ateles geoffroyi* (spider monkeys). Using network derived analyses to study the relationships among individuals over a succession of 8 years, they discovered that adult females formed tightly linked clusters that were stable over time. However, any immigrant adult females showed little association with any adult in the group (Ramos-Fernández et al. 2009). They therefore concluded that by virtue of their higher and more stable association, it is the females of a population that are central to the social structure of spider monkeys (Ramos-Fernández et al. 2009).

Henzi et al. (2009) conducted a study on two wild populations of *Papio hamadryas ursinus* (chacma baboons) over three consecutive seasons in South Africa. Social network analysis allowed them to test a previous assumption with regards to primate societies; that steady relationships between females will always be detectable and if such relationships are unable to be sustained, it is inevitable that the group will split into smaller daughter groups (Dunbar 1992). In contrast to this assumption, Henzi et al. (2009) discovered that when food is scarce, strong relationships were formed between females and high, persistent levels of association were seen between dyads. However, when food was readily available, the strong bonds identified previously by social network analysis in the food-scarce season were not maintained (Henzi et al. 2009).

Fischhoff et al. (2009) conducted a 4-year study on *Equus burchelli* (plains zebra) during which they looked at association levels among adult males and whether reproductive status affected bond formation between individuals and the social network of a population as a whole. An adult male can be classed as one of two categories; a bachelor with limited access to mates, or a stallion with a harem of females. Both are regularly found in the same herds, as harems and bachelors aggregate to form larger herds (Fischhoff et al. 2009). It was concluded that bachelors are more likely to be found in herds that contained a significantly higher proportion of adults than the herds in which stallions were more likely to be found and that associations formed between bachelors are much more stable than those formed between stallions, with bachelors forming cohesive sub-groups within a herd.

Vonhof et al. (2004) discovered a novel social structure among bats after gathering association data on *Thyroptera tricolor*, (Spix's disc-winged bats) in northeastern Costa Rica using mark-recapture data. Bats were captured from their roosts in young, rolled leaves of *Heliconia* or *Calathea* plants, each roost containing anywhere from 4 to 14 individuals of mixed sex. 85% of dyads maintained high levels of association for up to 100 days and 40% of dyads maintained long-term associations of a minimum of 420 days. Despite home ranges overlapping in space to a relatively high extent, members of differing social groups rarely associated with one another.

Using network analysis, Wolf et al. (2007) discovered a previously unknown complexity to the social structure of a colony of *Zalophus wollebaeki* (Galapagos sea lions). They studied the effects of age class, fine-scale site fidelity, and male territory distribution on the social organisation of a single population during the breeding season.

Network analyses revealed that the sea lion social system was comprised of three levels of complexity. All individuals were interconnected at the population level. This level could then be broken down into communities, which could then be broken down further into separate cliques. Wolf et al. (2007) were able to identify the factors influencing social structure at the population and community level to be sex and age class, and site fidelity, respectively. However, they were unable to account for the social structure seen within each of the cliques and therefore assumed these lower-level association preferences to be a result of genetic relatedness. Interestingly, male territories were not found to affect social structure on any level, but rather were superimposed on the structure formed by the females and their young (Wolf et al. 2007).

5.3 Temporal networks

By their very nature, animal social networks are dynamic in time and space, with individuals interacting or associating with one another at different times of day or in different seasons, and the fission and fusion of populations into larger and smaller groups. Time-ordered networks represent data observed for a set of interactions that occur at certain times, thereby retaining complete information on the ordering, duration and timing of events. While social network analysis has provided a useful tool for understanding the structure of social networks, it is less useful for understanding the temporal dynamics of these networks (Blonder et al. 2012). It is difficult to sufficiently study the flow of information between individuals and through populations using standard network analysis tools without making several key assumptions about the data. Such assumptions could include edges representing continual interactions; network structure being accurately and comprehensively recorded; interactions of interest being

sufficiently common and stable; and that the topology of the network is fixed (Blonder et al. 2012).

One method of overcoming the problems associated with the assumptions of a static network is to use a method of data analysis that takes network dynamics, such as the time and order of events into account. There are many methods of analysis available (see Blonder et al. 2012 for a detailed review), discussion of which is beyond the scope of this thesis. One such method is Network-Based Diffusion Analysis (discussed below and in greater depth in Chapter 6).

5.4 Network-based diffusion analysis

Network based diffusion analysis (NBDA) is a statistical technique pioneered by Franz and Nunn (2009) which allows non-random social transmission and other social effects on behaviour to be detected and quantified. Inference of social learning using NBDA results from comparing models that include social learning to models with only asocial learning to see if 'social-learning' models provide a better fit to the observed data than 'asocial-learning' models. When social learning is included in an NBDA model, the rate of social transmission between "informed" and "naïve" individuals is assumed to be proportional to the strength of the network connection between them.

As NBDA was only developed fairly recently, there are few published examples in which it has been used (Hoppitt and Laland, 2013). One application of NBDA has been published by Hoppitt et al. (2010a). The authors applied NBDA to data from an experimental study by Boogert et al. (2008) on the diffusion of the solution to a foraging task in starlings. In Boogert et al's original study, a randomisation technique failed to detect an association between the diffusion of the task solution and association.

However, upon the application of NBDA to the data, Hoppitt et al (2010a) found sufficient evidence for social transmission.

Webster et al. (2013) compared the effect of open and structured habitat structure on the transmission of foraging information through shoals of threespined sticklebacks. With the use of NBDA, the authors were able to establish that the location of foraging patches was not greatly affected by social transmission in an open habitat, however, there was strong evidence that social transmission occurred in a structured habitat and moreover that the transmission of information regarding the location of foraging patches followed the network structure of the shoals (Webster et al. 2013).

Another application of NBDA can be found in a study on lemurs by Kendal et al. (2010). However, in this case the authors failed to find evidence of social learning. NBDA has also been used in Chapters 6 and 7 of this thesis.

5.4 Summary

The study of network theory has been utilised widely by biologists with networks being present at a variety of biological levels. The social network structure of a group or population quantifies the pattern of interactions and relationships among its individuals. A variety of different phenotypic factors can generate non-random network structure within animal groups and the use of networks theory provides a number of useful metrics for quantifying the social structure of a population.

The study of animal social networks has the potential to provide of us with a wealth of knowledge concerning the behaviour of animals under a wide variety of contexts that

was previously inaccessible by other means including cooperation, disease transmission, social structure, and the role of individuals. NBDA can also be used to reveal any patterns of transmission of information through populations.

Chapter 6 is the first of two data chapters which use NBDA to study the transmission of information through populations of threespined sticklebacks under a foraging context.

Chapter 6. Information Flow Through Threespined Stickleback Networks Without Social Transmission

6.1 Introduction

Innovation can be said to occur when a new behaviour pattern is invented or when an existing behaviour pattern is modified to suit a novel context (Reader and Laland 2003). Behavioural innovation is an important facet of phenotypic plasticity enabling organisms to exploit new food sources, to improve their efficiency of utilising a familiar resource or to respond to other changes in their environment (Reader and Laland 2003). Social learning can lead to the transmission of behavioural innovations, potentially allowing innovations to spread rapidly through populations (Hoppitt et al. 2010a). There are a large number of studies that have reported innovations and novel behaviour patterns spreading through populations (Laland & Galef, 2009; Lefebvre 1995a, 1995b; Reader, 2004; Zentall & Galef, 1988). The most famous examples being Japanese macaques washing sweet potatoes (Kawai 1965) and British titmice opening milk bottles (Fisher and Hinde 1949; Hinde and Fisher 1951).

Despite extensive recent research into animal social learning (Heyes 1994; Heyes and Galef 1996; Box and Gibson 1999; Rendell et al. 2011), the social factors influencing learning of innovations by individuals in freely interacting groups remain poorly understood (Coussi-Korbel and Fragaszy 1995; Reader and Laland 2000; Boogert et al. 2008). It is commonly supposed that social learning, where it occurs, results in social transmission, i.e. where performance of a behaviour by one individual makes it more likely that other individuals will add the behaviour to their repertoires. However, in most cases in which the spread of a behavioural innovation has been reported in natural or captive populations, the possibility cannot be excluded that either asocial learning

caused the observed change in behaviour, or that the learned behaviour of one individual facilitates acquisition of behaviour by others in more subtle ways than are normally considered (Galef 1992; Reader 2004; Hoppitt et al. 2010b).

Furthermore, many previous theoretical and empirical studies have tended to assume that all members of a population are equally likely to transmit or receive information (Reader and Laland 2000). Although animals might pay equal attention to the actions of each group member, Coussi-Korbel & Fragaszy (1995) suggest that this is unlikely and that, to the contrary, animals within a group are more likely to learn from some individuals than from others. Indeed, this notion of 'directed social learning' suggests that animals might either copy strategically, for instance, by attending to the behaviour of older or more successful individuals (Laland 2004) or might copy their nearest neighbours (e.g. Ballerini et al. 2008). The social network therefore has the potential to greatly influence the transmission of innovations through a population. A higher level of association between some individuals than others is likely to give rise to a higher probability of social learning taking place.

Network-based diffusion analysis (NBDA; Franz & Nunn 2009) is a recently developed method of data analysis of potential use in the field of animal social learning that allows non-random social transmission, as well as other social effects on behaviour to be detected and quantified. Here we apply NBDA to captive groups of threespined sticklebacks presented with either one or two foraging tasks, to provide evidence of any non-random patterns of social influence on task discovery and solution within shoals.

In NBDA, the rate that individuals move from a naïve to an informed state (having solved a task) is modelled as a function of the total of their network connections to informed individuals. Thus, NBDA implicitly assumes that social learning will be

manifest as social transmission. However, in a foraging task social influences other than social transmission might operate independently to decrease either the latency with which naive individuals discover the task or the latency with which they subsequently solve it. Furthermore, a fully informed individual who has solved a task might exert more influence on the naive than an individual who has merely discovered that task. To investigate such possibilities, we extend the NBDA model to multiple states, analysing the process of task solution as comprising two identifiable stages, discovery and solution, thus allowing specific types of social influences on each to be both detected and quantified.

6.2 Methods

6.2.1 Subjects and apparatus

Subjects were 160 threespined sticklebacks maintained in 16 groups of 10, with 8 groups used in each experiment. We used no individuals displaying signs of nuptial colouration or gravidity, as reproductive state has been shown to affect an individual's reliance on social learning in sticklebacks (Webster and Laland 2011).

To encourage size-assortative shoaling (Krause 1993b), and thereby to promote heterogeneity of social network structures, we deliberately generated variation in body size within groups. Individuals ranged from 38 to 71mm in length with an overall mean within-group range of 14.8mm.

We captured subjects using mesh cage traps from the Kinnessburn, St Andrews, U.K. (56°20'05"N; 2°47'14"W) between June and September, 2010 and held them in groups of 40 in 60 L tanks at a temperature of 8°C, and fed them daily with frozen chironomid (*Chironomus* sp.) larvae for a minimum of 2 weeks before testing (July to October 2010).

We tested groups of 10 individually marked fish (Webster and Laland 2009) in a rectangular black test tank measuring 60x80cm. To ensure that vertical distance within the water column between individuals did not confound estimates of inter-individual distances measured from above, we filled the test tank with filtered tap water to a depth of only 5 cm. The test tank had a gravel substrate 1cm in depth, and 10 black, pyramid-shaped obstacles (measuring 10cm diam. at the base and 6cm high) placed at regular intervals throughout the tank (see Figure 6.1) allowing only associating individuals to see one another whilst allowing the experimenter to view all fish. We filmed each test trial using a Canon HG20 video camera held 1.2 m above the test tank.

We conducted both one-task and two-task experiments, involving identical foraging tasks, comprised of a transparent cylindrical tube measuring 24 cm in length and 7 cm in height placed horizontally on the gravel substrate at each end of the test tank. We inserted 15 ml of defrosted chironomid larvae suspended in water into one end of the tubes, which had 15 small holes (2 mm diam.) allowing olfactory cues from larvae to escape. The other end of each tube was open and its circumference clearly marked with black electrical tape. Consequently, although fish could see and smell food at both ends of each tube, they could gain access to food only at one end (see Figure 6.1).
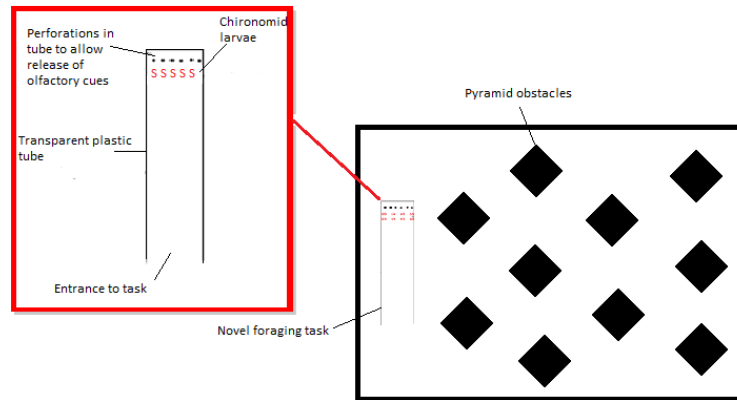
Figure 6.1: A plan view of the experimental tank after the addition of the task in the one-task experiment with an up-scaled diagram of the novel foraging task.

We predicted that diffusion of information regarding both the location of food and the solution to the tasks would be influenced by the social network, with individuals that had a high level of association with one another being more likely to discover and solve the tasks in succession and with more similar latencies than individuals that had a low level of association.

6.2.2 Procedure

6.2.2.1 Determining the network structure

To describe social networks, for each experiment, we individually placed each of eight groups of 10 fish into the test tank and allowed each group to settle and explore the tank for a period of 15 min before filming for 2 hr. We subsequently took point samples from the film at 6-min intervals, giving a total of 20 observations for each group.

We defined individuals as associating if they were within four body lengths (defined as the mean body length of a group's members) of one another from head to head, a distance generally accepted as indicative of shoaling in fishes (Pitcher and Parrish 1993). We then created an association matrix based upon the proportion of point

91

samples that each fish was observed to be within four body lengths of each of the other fish in its group.

To test for within-group association networks, we calculated the sum of the squared difference in association strength from the mean association strength for the group (the 'test statistic'). This value would be larger than a null distribution if individuals were associating non-randomly. To generate the null distribution, we randomised the identity of each fish across observations and recalculated both the association network and sum of squared differences for the randomized group. To calculate a p value, we determined the proportion of the null distribution that was greater than or equal to the observed test statistic.

6.2.2.2 Testing for social learning

At the end of the 2-hr filming of a group, we introduced the foraging tasks and filmed the group for a further 45 min, after which the trial ended and we removed all fish from the experiment. We recorded both the latency with which each individual first discovered each task (defined as occurring when an individual was seen striking at food through the transparent tube) and the latency with which each individual first solved each task (defined as consuming food within the tube). We scored only the first 20 min of video footage after the first fish in each group solved each task at which time food items were still visible inside the tube in all trials.

In addition to recording the latency for discovery and solution of the tasks, we also recorded the latency with which each fish entered an arbitrary area (measuring 20 cm x 10 cm) within the tank. This control location contained no food and no distinctive topographical features. In our analysis, we compared inter-individual latencies to

"discover" the control location with similar latencies to discover the tasks. This comparison allowed us to distinguish between effects of affiliation and effects of exposure to individuals in the vicinity of the tasks.

6.2.2.3 Network Based Diffusion Analysis

We used Network Based Diffusion Analysis (NBDA) (Franz and Nunn 2009; Hoppitt et al. 2010a) to determine whether the sequence with which subjects discovered and or solved the tasks was correlated with the pattern of association observed between individuals in a group (i.e. the social network).

We used the order of acquisition diffusion analysis (OADA) variant of NBDA (Hoppitt et al. 2010a), which is sensitive only to the order in which individuals acquire a trait, not to latencies of acquisition (see Appendix 1 for justification). We analyzed order of acquisition across all groups, treating the data from all eight groups as a single diffusion network, with zero network connections between individuals in different groups. This treatment of the data renders the OADA sensitive to between-group differences. If consecutive discoverers/solvers tend to be from the same group, this is consistent with the hypothesis that they are learning from each other.

We also modified the OADA model to allow for multiple states (see Appendix 1 for details). Existing NBDA approaches assume that individuals move directly from a 'Naïve' to 'Informed' state when they first solve a task (Hoppitt and Laland 2011). Here we wished to tease apart social effects influencing the rate at which individuals discovered and solved the task (c.f. Boogert et al. 2008). We assumed that at any given time an individual could be in one of three states: 'Naïve' (has not discovered the task), 'Discovered' (has discovered the task), and assumed further that Discovered individuals could be either a 'Non-solver' (has not solved the task) or 'Solver' (has solved the task).

93

Each task was treated separately in the two-task experiment, for example an individual could be classed as a 'Solver' for the left hand task, however, could still be 'Naïve' for the right hand task.

We fitted separate OADA models for: (i) the rate at which naïve individuals discovered the task, and (ii) the rate at which 'discovered' individuals solved the task (see Appendix 1). We allowed for the fact that both rate of discovery and rate of solving might be affected by network connections to individuals that: (i) had discovered the task; or (ii) had solved the task.

We also included body length as an individual-level variable (entered as a difference from group mean body length) and treated 'group' as a factor, to allow for the possibility that groups might differ in their rates of asocial discovery or solving. We considered social learning and group differences in asocial rates of learning as alternative explanations for differences between groups and consequently did not include both variables in the same model although we considered models including all other possible combinations of variables.

Instead of using a model-selection procedure to choose a best model, we used a model averaging approach, using Akaike's Information Criterion, corrected for sample size (AICc) (Burnham and Anderson 2002). Inferences based on model averaging take into account uncertainty as to which model is best. AICc estimates the Kullback-Leibler (K-L) information for a model (i.e. the extent to which the predicted distribution for the dependent variable approximates its true distribution). The AICc allows us to calculate an Akaike weight for each model that gives the probability that the model is the actual best K-L model (that with the lowest K-L information) out of those considered, allowing for sampling variation. By summing Akaike weights for all models that

include a specific variable, we obtain the probability that a variable is in the best K-L model, thus quantifying support the data give for an effect of a variable (Burnham and Anderson 2002).

This approach is preferable to calculating a p value to quantify the strength of evidence for each effect, because: (i) the p value depends on which model is chosen and consequently does not account for model uncertainty, and (ii) a large p value tells us little about the strength of evidence against an effect (i.e. whilst statistical power can be calculated, the power has to be for specified, usually arbitrary, effect sizes (Johnston 1999)). Therefore, for each variable considered, we give its total Akaike weight (as a %) and model averaged estimate (Burnham and Anderson 2002). We also provide unconditional 95% confidence intervals using Burnham and Anderson's (2002) method for adjusting profile likelihood confidence intervals for model selection uncertainty.

6.2.2.4 Comparison of network-specific and homogeneous effects

Our OADA analysis is sensitive to between-group differences in discovery and solving times. Consequently, evidence of an effect of network connections to other 'discovered' and/or 'solved' individuals might reflect an effect that operates equally among all individuals in each group, rather than an effect that follows the social network. To tease apart network-specific and homogeneous (i.e. non-network-specific) effects, we fitted alternative versions of models for rate of discovery and for solving. To reduce the set of models to be fitted, we constrained all models to include effects for which there was more support for than there was against (>50%). To assess whether each social effect operated homogeneously within groups (i.e. independent of patterns of association), we replaced the social network with a homogeneous network (connection of strength 1 for individuals in the same group, 0 for those in a different group) for each effect. We also

allowed for the possibility of network-specific and homogeneous components to each effect (see Appendix 1 for details).

6.2.2.5 Social transmission versus an untransmitted social effect

NBDA was designed such that evidence for $s > 0$ could be used to infer social transmission of a trait. However, an $s > 0$ need not indicate social transmission of discovery of a food patch. Closely associated 'undiscovered' individuals might discover the food source at a similar time simply because they tend to move about together, and movement in a group is distinct from social transmission. In social transmission, one individual discovering a food patch causes associated individuals to discover the food patch sooner than they otherwise would. In contrast, we refer to the simultaneous discovery of a food patch by naive individuals moving in a group as an "untransmitted" social effect. The key distinction here is that, in the case of social transmission, knowledgeable individuals pass on some of their knowledge to others, whereas with an untransmitted social effect the individuals that facilitate learning in others are uniformed. Perhaps slightly confusingly, such untransmitted social effects often meet accepted definitions of social learning (Heyes 1994), which encompass any social process that facilitates learning in others. Note that simple movement in a group can account only for an apparent social transmission effect on the rate of discovery, not on the rate of solving.

To separate untransmitted and transmitted social effects, we reasoned that untransmitted social effects would be seen whenever individuals first entered any arbitrary area within the test arena. As mentioned in the Methods, we identified an arbitrary control patch that contained no food in the test arena and recorded the time at which each individual in each group first entered the control patch. We then treated these data as an additional

96

set of diffusions, and estimated the *s* parameter for both control and real patches, i.e. s_R and s_C respectively. We then estimated the strength of social transmission as the difference in *s* parameters between real and control patches (s_R - s_C). We included only body length as an additional covariate in this analysis since body length was strongly supported by the Akaike weights (see Table 1a).

6.3 Results

6.3.1 Two task experiment

Individuals in six of the eight groups were found to be associating with others significantly differently from chance expectations (P = 0.001 to 0.047), whilst the other two groups (P = 0.073 and 0.196 respectively), had less heterogeneous networks.

6.3.1.1 First discovery

There were no trials in which all individuals within a group discovered both tasks, with the number of discoverers of each option ranging from 3 to 8. A minimum of seven individuals discovered one or the other of the tasks with 112 first discoveries across both individuals and tasks. Diffusion curves for discovery time (Figure 6.2c) generally reveal a rapid increase in the number of individuals discovering one or both tasks after initial discovery by one individual.
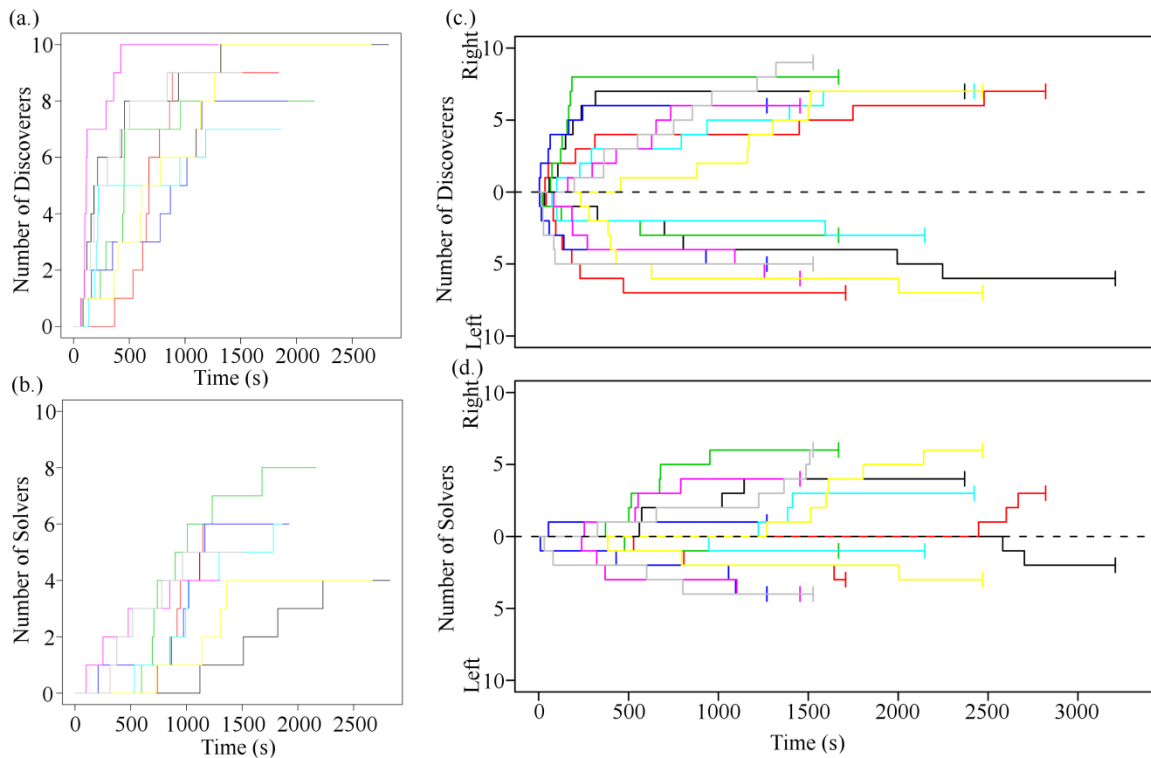
Figure 6.2: The diffusion curves for the times of (a) first discovery in the one-option task, (b) first solving in the one-option task, (c) first discovery in the two-option task, and (d) first solving in the two-option task. The two-option diffusion curves show times for both the left- and right-hand tasks. Each colour represents a different group.

Both estimates from the NBDA and support for each variable are shown in Table 6.1a. There was strong evidence (total Akaike weight = 97.8%) that being well connected to others who had already discovered a task increased the probability that a naïve individual would be the next to discover that task, providing clear evidence of social learning. The magnitude of this effect was estimated to be a linear increase of 1.5 times (95% CI= [0.32, 4.4]) the average asocial rate of discovery for every unit of network strength. However, there was no evidence for social transmission of the patch location, with the contrast between real and control food patches (s_R-s_C) estimated at -2.48 (95% CI: [-11.0,1.4]), a result in the opposite direction to that expected if social transmission were occurring. The present finding that effects of group membership at

real patches were not greater than those at control patches suggests that the social effect on discovery may be a result of associated individuals encountering the task at approximately the same time because of their influence on each other's movements. There was little evidence that being well-connected to solvers of a task facilitated discovery of that task, and strong evidence against an effect of connectedness to discoverers generalising across tasks, implying that discovery was a location-specific effect.

Surprisingly, there was some support for the hypothesis that individuals were more likely to discover a task next if they were well connected to individuals who had solved the other task than if they were not so connected. This effect was estimated to be similar in magnitude to the task-specific effect of discovers (1.4, 95% CI= [0.20,6.5]). There is also support for an effect of body length, with larger individuals being more likely than smaller individuals to discover a task first, as well as evidence that individuals that had discovered one task were less likely to discover the other (see Table 1a for estimated effects and confidence intervals).

6.3.1.2 First solve

In all 8 trials, each task was solved by at least one individual within the allotted time with 6 individuals solving the task in 3 of the groups and a total of 39 first solves across all individuals and tasks. Again, discoverers did not move food items outside of the tube.

As confirmed by the NBDA analysis, diffusion curves for the solving times of the foraging tasks (Figure 6.2d) show individuals solving both tasks at fairly regular intervals rather than in collective bursts, suggesting that solvers were not influenced by other solvers.

Both estimates from the NBDA and support for each variable are shown in Table 6.1b. Probably as a result of the low number of total solvers (39 of 80 subjects), there is no strong support for any one effect. However, total support for models in which at least one social effect is operating is high (93.3%), and there is little support for the alternative hypothesis of underlying group differences in rate of discovery of the two tasks. A likely explanation for the pattern of data is that individuals that had already discovered one task and were closely connected to other discoverers of that task were more likely to solve that task than other individuals (support= 77.9%), with the effect estimated at 3.9 (95% CI=[0.334, 590]). There is also some evidence for an effect of body size on solving, with smaller individuals who had already discovered a task tending to solve it sooner than larger discoverers.

6.3.1.3 Comparison of network-specific and homogeneous effects

Support for models that included social effects on learning, either specific to the social network and/or non-network-based group effects, is shown in Table 6.2. There is a fairly clear indication that, if there is a social effect on the rate at which discoverers first solve the task, it follows the social network (support= 88.5%). Effects of the social network are less clear on the rate at which naïve individuals discover the task. Possibly, individuals are attracted to a task by strongly connected individuals that have already solved a task, and consequently, are more likely to return to that task and/or remain near it than individuals weakly connected to solvers, making it likely that they will solve that task more rapidly than individuals only weakly connected to solvers. Counteracting this effect is evidence for a second process whereby, when many individuals in a group have solved a task, those group members that had not yet discovered the alternative task are more likely to do so, perhaps because the popular task becomes too crowded to solve. In either case, there is clear evidence of social learning.

Table 6.1a: Two task NBDA results for naïve -> discovered

Variable	d.f.	Support (sum of Akaike weights)	Model averaged effect estimate	Unconditional 95% confidence interval
Total network connection to discoverers: task specific	1	97.8%	1.4	[0.32, 4.4]
Total network connection to discoverers: cross task	1	5.6%	0.007	
Total network connection to solvers: task specific	1	24.2%	0.094	
Total network connection to solvers: cross task	1	75.4%	1.4	[0.20,6.5]
Body length (mm)	1	91.3%	0.048	[0.016,0.096]
Bias towards right task	1	26.3%	1.0x	
Group	7	1.1%	1.0x	-
Discovered other task	1	81.8%	0.29x	[0x, 0.78x]
Solved other task	1	32.7%	0.02x	

Table 6.1b: Two task NBDA results for discovered non-solver -> solver

Variable	d.f.	Support (sum of Akaike weights)	Model averaged effect estimate	Unconditional 95% confidence interval
Total network connection to discoverers: task specific	1	79.9%	3.9	[0.334, 590]
Total network connection to discoverers: cross task	1	26.5%	0.38	-
Total network connection to solvers: task specific	1	6.8%	0.048	-
Total network connection to solvers: cross task	1	12.6%	0.087	-
Body length (mm)	1	82.4%	-0.171	[-0.94,-0.0049]
Bias towards right task	1	28.6%	1.1x	
Group	7	<0.1%	1.0x	-
Discovered other task	1	30.3%	1.2x	
Solved other task	1	47.2%	1.9x	

Shaded cells indicate there was more support for an effect than against (>50%). Social effects are estimated relative to the mean rate of asocial discovery, e.g. the 1.4 in Table 6.2a signifies that an average individual with one unit of total association to discoverers of a task is 2.4x faster to discover the same task than an average individual with no connections to discoverers of that task. The effect of body length is estimated as the logarithm of the multiplicative difference per mm in body size (standard in modelling rates), e.g. in Table 6.2a 0.048 indicates that the asocial rate of discovery for a fish of 50mm would be exp (5x 0.048) = 1.27x greater than that for a fish of 45mm. For all other effects we give the estimated multiplicative difference in rate, for group this is for the most extreme groups. Unconditional 95% confidence intervals were calculated using a computationally intensive profile likelihood procedure (see Appendix 1) so we only calculated these for variables with support >50%. The effect of association to solvers is estimated as the effect over and above that of their effect as discoverers. Likewise the effect of having solved the other task is estimated as the effect over and above the effect of having discovered the other task.

Table 6.2: Support for models in which social effects are assumed to follow the social network, act homogeneously within groups, or as a combination of the two in the two-task experiment. "Total network-specific" support quantifies the level of support for models in which network connections influence the strength of each social effect.

	Support (sum of Akaike weights)			
	Network (1 d.f.)	Homogeneous (1 d.f.)	Both (2 d.f.)	Total network-specific
Naïve -> discovered				
Total network connection to discoverers: task specific	44.5%	35.7%	19.8%	64.3%
Total network connection to solvers: cross task	39.6%	43.9%	16.5%	56.1%
Discovered non-solver -> solver				
Total network connection to discoverers: task specific	56.9%	11.5%	31.6%	88.5%

6.3.2 One task experiment

Individuals in all groups were found to associate with others at proportions significantly different from chance ($P = <0.001$).

6.3.2.1 First discovery

In four groups, all individuals made contact with the task, whilst in the other four groups 7 to 9 of their 10 members did so. Diffusion curves for discovery can be seen in Figure 6.2a. Both estimates from the NBDA and support for each variable are shown in Table 6.3a. There was strong support across groups for the hypothesis that naïve individuals who were well connected to others who had discovered the task were more likely than were individuals who were weakly associated with discoverers to be the next to discover it themselves (total Akaike weight= 99.8%, see Table 6.3a for estimated effects) providing clear evidence of social learning. However, there was no strong evidence for social transmission of patch location, with the contrast between real and

control food patches (s_R-s_C) estimated at 1.84 (95% CI: [-3.9,11.3]). There was also little evidence that association with task solvers facilitated discovery of the task (total Akaike weight= 19.8%) and little support for an effect of body length on rate of discovery (total Akaike weight= 48.5%). These findings suggest an untransmitted social effect underpinning the observed diffusions of task discovery.

6.3.2.2 First solve

In all 8 groups, a minimum of 4 fish solved the task within the allotted 20 min after first solution in a group. No scrounging was observed, as solvers did not move food items outside the tube. Diffusion curves for solving can be seen in Figure 6.2b. As can be seen in Table 6.3b, which shows estimates from the NBDA and support for each variable, social transmission did not influence the rate at which individuals solved the task either individually or as a group. However, there was also no support for models containing neither of these effects (total Akaike weight= 31.7%), suggesting that there may be some important difference between groups, the nature of which we could not resolve in this analysis.

6.3.2.3 Comparison of network-specific and homogeneous effects

No other variables were included in the model since none had support >50%. The results clearly support the social network (support= 98.8%) over the homogeneous model. As with the two-task experiment, we also fitted a model with a network and homogeneous effect but the homogeneous effect was estimated at 0, meaning that this model is effectively the same as the network model.

Table 6.3a.NBDA results for naïve -> discovered transition

Variable	d.f.	Support (sum of Akaike weights)	Model averaged effect estimate	Unconditional 95% confidence interval
Total network connection to discoverers	1	99.8%	4.0	[1.17,12.7]
Total network connection to solvers	1	19.8%	0.081	-
Body length (mm)	1	48.5%	0.018	-
Group	7	0.2%	1.0x	-

Table 6.3b. NBDA results for discovered non-solver-> solver

Variable	d.f.	Support (sum of Akaike weights)	Model averaged effect estimate	Unconditional 95% confidence interval
Total network connection to discoverers	1	16.4%	0.006	-
Total network connection to solvers	1	21.5%	0.042	-
Body length (mm)	1	30.0%	0.007	-
Group	7	35.8%	2.0x	-

Shaded cells indicate there was more support for an effect than against (>50%). Social effects are estimated relative to the mean rate of asocial discovery, e.g. the 4.0 in Table 6.3a signifies that an average individual with one unit of total association to discoverers is 5x faster to discover the task than an average individual with no connections to discoverers. The effect of body length is estimated as the logarithm of the multiplicative difference per mm in body size (standard in modelling rates), e.g. in Table 6.3a 0.018 indicates that the asocial rate of discovery for a fish of 50mm would be $\exp(5 \times 0.018) = 1.09x$ greater than that for a fish of 45mm. For group we provide the estimated multiplicative difference in average asocial rate between the most extreme groups. "Unconditional" 95% confidence intervals were calculated using a computationally intensive profile likelihood procedure (see Appendix 1) so we only calculated these for variables with support >50%. The effect of association to solvers is estimated as the effect over and above that of their effect as discoverers.

6.4 Discussion

We present one of the first examples of network-based diffusion analysis of the behaviour of nonhuman animals. By breaking the processes of task solution into identifiable stages, specific types of social influences were both characterised and quantified.

6.4.1 Discovery

We found strong evidence in both the one-task and two-task experiments for a social effect of the discovery of the novel foraging tasks, with individuals tending to discover a task sooner when others in their group had previously done so. However, overall we find no evidence that this effect is the result of the task location being socially transmitted between individuals, since the social effect on "discovery" of an arbitrary empty control patch appeared as strong as discovery of a patch where foraging was possible. These findings suggest that an untransmitted social effect underlies the observed diffusions - almost certainly the influence of fish on one another's movements.

We note that, in the absence of NBDA, most researchers would have interpreted the evidence of diffusion along a social network as indicative of social transmission, although the possibility of asocial learning underlying diffusions has long been recognized (Lefebvre, 1995; Reader, 2004; Hoppitt et al., 2010b). Here, use of NBDA provided evidence for a third possibility: the social learning of task location in the absence of social transmission. There is unambiguous evidence for both learning and a social influence on latencies to learn, but no evidence of social transmission. The social effect on "discovery" of an arbitrary empty control patch appeared as strong as the social effect on discovery of the tasks.

A number of previous studies of social learning in fish that report social effects consistent with local enhancement but equally consistent with the hypothesis of a mutually reinforcing tendency of individuals that have discovered a potential food source to remain near that food source and eventually learn to exploit it (eg. Baird et al. 1991; Laland and Williams 1997; Day et al. 2001; Webster and Hart 2006). The present findings are of particular significance in that they draw attention to the possibility that many natural diffusions may similarly result from untransmitted social effects rather than from either social transmission or asocial learning.

6.4.2 Solution

Our findings also provide little evidence of social transmission of solution to the task. In both the one-task and two-task experiments, a higher level of association with previous solvers did not predict a higher rate of solving the task and gaining access to food. Social transmission would require that association with those that had solved the task leads to a higher rate of transition from a naïve to an informed state: either increasing the rate of discovery or the subsequent rate of solving. Here we find evidence of neither. Nonetheless, we did find evidence of a social effect on solving the task; a higher degree of association with those that had previously discovered the task predicted a higher rate of solving it.

Unexpectedly, in the two-task experiment, we found that associating with others that have previously solved one task leads to an increased rate of discovery of the remaining task. Two processes, stimulus enhancement and competition, provide plausible explanations. Stimulus enhancement (Spence 1937) is a process similar to local enhancement. However, in cases of stimulus enhancement individuals attract the attention of others not to a particular location but to a class of objects. Because the two

tasks were identical, stimulus enhancement of one task would have led to increased attention to the other. Alternatively, when one of the tasks had attracted many foragers, remaining individuals may have sought an alternative foraging location where there was less completion for food.

6.4.3 Size effects

An individual fish's size was found to have a significant effect in the two-task experiment, with larger fish being more likely to discover the task first and smaller fish being more likely to solve the task first. However, this finding was not observed in the one-task experiment. The difference between the one-task and two-task diffusions may be explained by the fact that, as a result of the sizes of fish available when we initiated each experiment, the size range within each group was smaller in the one-task experiment (mean within group difference of 12.5 mm) than in the two-task experiment (mean within group difference of 17.1 mm). Larger fish are known to be more likely to be at the front of a shoal and have a greater influence over others than smaller fish. For example, Reebs (2001) demonstrated that a minority of large golden shiners were able to lead smaller fish to a known foraging patch. However, when smaller fish acted as leaders the group did not follow. Another possible explanation for the observed difference is simply due to the fact that the larger fish are able to cover a greater area than smaller fish within a given time due to faster swimming speeds. They are therefore more likely to discover the location of the task at a faster rate, as was found by Day et al. (2001) amongst shoals of guppies.

However, it was also observed that smaller individuals were significantly more likely than larger individuals to solve the task first, a finding also reported in guppies (Laland & Reader 1999). Small fish often have a higher motivation to feed than large fish due to

lower metabolic efficiency (Weatherley and Gill 1987; Wootton 1994) and might therefore be more likely to both persevere in their attempts to access food than larger fish and to find a solution to the task.

6.5 Summary

Our results suggest that social influences on learning can be strong, even without direct transmission of information (e.g. patch locations or task solutions) between individuals. Individuals within each group tended to discover a food patch sooner when others in their group had previously done so, but this temporal pattern of discovery did not appear to be a result of social transmission *per se*. Rather, the tendency of fish to travel in groups resulted in increased simultaneity of discovery, followed by individual learning of the solution. Knowledge as to how to solve a task and acquire food did not spread from informed to uninformed individuals; rather uninformed individuals learned together, but nonetheless benefited from the elevated rate of patch discovery associated with social foraging. The fact that these results are replicated in both the one-task and two-task experiments gives significant strength to our arguments. The methods of analysis employed here could be widely used by those studying diffusion of social information through populations to provide finer characterization of the nature of social influences on diffusion of innovations through social groups.

Chapter 7 uses a similar methodology and analysis to study the effect of familiarity on transmission of information through populations of threespine sticklebacks.

Chapter 7. Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals

7.1 Introduction

In this study we sought to determine the role of fine-scale social organisation in determining patterns of information diffusion using NBDA of the foraging behaviour of groups of threespine sticklebacks that contained both familiar and unfamiliar individuals. In many species of fishes, active preferences for associating with familiar individuals have been shown to strongly affect social organisation (Ward and Hart 2003; Griffiths and Ward 2011). Broadly speaking, familiarity operates via at least two mechanisms (Ward et al. 2009). The first is based upon learned recognition of other individuals. After a period of continuous interaction, fish come to remember the identity of their shoalmates, and prefer to group with them over other conspecifics with whom they haven't previously interacted (e.g. Griffiths &Magurran 1997, reviewed by Griffiths & Ward 2011). Familiarity also occurs via a more general mechanism based upon self-referent matching, whereby fish prefer to associate with individuals that have recently eaten the same prey or occupied similar habitat types to themselves (Olsen et al. 2003; Ward et al. 2004; 2005; 2007; 2009; Webster et al. 2008a; 2008b; 2009). While the precise mechanism behind this mechanism of recognition is not fully clear, it potentially operates via diet- or habitat derived amino acids or other metabolites released via the gills (in freshwater), or through the urine or epidermal mucus of the fish (Bryant &Atema 1987; Courtenay et al. 1997; Moore et al. 1994; Matsumura et al. 2004; Olsen et al. 1998).

Learned familiarity has been shown to play a role in directing the transmission of information between guppies under binary choice conditions. In a study by Lachlan et al. (1998), individual adult guppies were presented with two shoals of conspecifics, consisting of either familiar or unfamiliar individuals. When given the choice of following either shoal to opposite ends of the tank, it was seen that focal guppies were more likely to follow the shoal comprised of familiar rather than unfamiliar fish. Such behaviour is likely to lead to information acquisition and social learning, for example, if following conspecifics to a food source. A further study on guppies by Swaney et al. (2001) tested the hypothesis they would learn more effectively from familiar than unfamiliar demonstrators that had been trained to swim a particular route to a food source. The trained demonstrators were placed with small shoals of untrained observers. It was revealed that untrained individuals were more likely to discover and subsequently learn the route to the food source when demonstrators were familiar to them than when they were unfamiliar. This suggests that familiarity between individuals can influence social learning, with individuals learning more effectively from familiar conspecifics.

In nature, given the fission-fusion dynamics seen to occur in many systems (e.g. Croft et al. 2003), it seems likely that groups will exist that contain both familiar and unfamiliar individuals. Until relatively recently the statistical tools to quantify the effects of factors promoting differences in fine-scale social organisation, such as differences in familiarity, upon patterns of information transmission in free-ranging groups did not exist. The recent development of network-based diffusion analysis (NBDA, Franz & Nunn 2009; Hoppitt et al. 2010), which allows non-random transmission of information to be detected, means that the importance of such factors can now be accounted for quantitatively. Indeed, recent research has demonstrated that NBDA is an appropriate

and flexible method for quantifying diffusion. It has been deployed to address questions about the diffusion of information and novel behavioural innovations in a range of species, including fishes, birds, and among mammals in herpestids and cetaceans, both in the laboratory and in the wild (Allen et al. 2013; Aplin et al. 2012; Atton et al. 2012; Hoppitt et al. 2012; Webster et al. 2013).

Sticklebacks exhibit familiarity through both learned recognition (Frommen et al. 2007b) and through recognition of habitat- and diet-derived cues (Ward et al. 2004; 2005; 2007; Webster et al. 2008b). In this study our primary aim was to determine the role, if any, of familiarity in driving directed transmission of information. The precise mechanism by which familiarity occurred was of less concern. For this reason, in order to maximally differentiate familiar and unfamiliar fish, we used a protocol which allowed for familiarity to occur via both learned and resource-derived recognition. We adopted the approach of Chapter 6 (Atton et al. 2012), in which groups of sticklebacks were placed into an arena and allowed to search for and feed upon prey placed within novel feeder apparatuses. We tested the following predictions: (1) That the social network structure of groups of sticklebacks would be influenced by familiarity. Specifically, we expected to see more frequent patterns of association between familiar fish than between unfamiliars. (2) That information would diffuse via association networks, with greater likelihood of transmission between more strongly associated individuals. (3) Stemming from this, we expected to see that individuals would be more likely to acquire information about the location of feeder apparatuses and how to access them from familiar groupmates, than from unfamiliar individuals.

7.2 Methods

7.2.1 Subjects and treatment groups

Threespined sticklebacks were captured from the Kinnessburn, a small stream in St Andrews, U.K. (56.33.4925 N, 22.78.8151W) using mesh cage traps in April 2012 and held in two groups of 40 in 90 L tanks at a temperature of 8°C in our laboratory. The fish were fed daily with frozen bloodworms (*Chironomus*sp. larvae) for two weeks immediately following capture. After this initial holding period two groups of 40 individuals were switched to separate, novel diets for one month. One group was fed exclusively on *Artemia* and the other group exclusively on *Tubifex*. At the end of this period we had two groups that had been held separately for six weeks, enough time for learned within-group familiarity to become established in this species (Ward & Hart 2003), and which had been fed on different diets for four weeks, which is sufficient for familiarity based upon diet-derived cues to develop (Ward et al. 2007; Webster et al. 2007). Hereafter, fish taken from the same holding tank are referred to as 'familiar' and fish from different holding tanks as 'unfamiliar'.

From these fish we formed seven replicate groups each containing 10 individually marked fish to use in the foraging diffusion experiment. No individuals that were displaying signs of nuptial colouration or gravidity were used, as reproductive state has been shown to affect an individual's reliance on social information in sticklebacks (Webster and Laland 2011). Each fish was marked with a unique non-invasive disc-tag attached to its first dorsal spine, as described in Webster &Laland (2009). Each group of ten fish contained five fish from the *Artemia*-fed treatment and five from the *Tubifex*-fed treatment, selected haphazardly from their holding tanks. Individuals within each

group were size matched to within 4mm of one another. No fish was tested more than once.

7.2.2 Test arena and procedure

Each group was tested separately in a rectangular black test tank measuring 60x80 cm. To ensure that vertical distance within the water column between individuals did not confound estimates of inter-individual distances, described below, we filled the test tank with filtered tap water to a depth of only 5 cm. The test tank had a gravel substrate 1cm in depth, and 10 black, pyramid-shaped obstacles (measuring 10cm square at the base and 6cm high) placed at regular intervals throughout the tank (Figure 6.1) to provide a degree of structural complexity, whilst allowing the experimenter to view all fish at all times. The test tank was held within a shelter to minimize outside disturbance. Two 60 watt fluorescent strip lights were used to provide illumination. We recorded each test trial using a Canon HG20 video camera fixed 1.2 m above the test tank above a small filming hole.

In the second phase of the trial, described below, bloodworm prey were presented within two identical feeding apparatuses, hereafter referred to as foraging tasks. These consisted of transparent cylindrical tubes, accessible from one end, measuring 24 cm in length and 7 cm in diameter placed horizontally on the gravel substrate at each end of the test tank (see section 6.2.1). We inserted 15 ml of defrosted bloodworms suspended in water into the closed end of the tubes, which had 15 small holes (2 mm diameter), allowing chemical cues from bloodworms to escape. At the open, accessible end of the tube, the entrance was clearly marked with black electrical tape around its

circumference. Consequently, although fish could see and smell food at both ends of each tube, they could gain access to food by entering it from one end only.

Fish were tagged two hours before the trial began. The group of ten fish was then added to the test tank and allowed to settle for 15 minutes. Following this the trial began. The trial had two phases, an association phase, which we used to quantify social network structure, and the foraging phase, from which we extracted data to perform the NBDA. The association phase ran for 120 minutes. From the recording of this phase we point sampled the shoaling behaviour of the fish at six-minute intervals, giving a total of 20 observations for each group. If individuals were within four body lengths of one another (defined as the mean body length of the groups' members) from head to head, a distance generally accepted as indicative of shoaling in fishes (Pitcher and Parrish 1993), they were classed as shoaling. Using this data we created an association matrix for each group based upon the proportion of point samples that each fish was observed to be within four body lengths of each of the other fish in its group.

Following the 120-minute association phase, we carefully introduced the foraging tasks and filmed the group for a further 45 minutes, after which the trial ended and we removed all fish from the experiment. We recorded both the latency with which each individual first discovered each task (defined as occurring when an individual was seen striking at food through the transparent tube) and the latency with which each individual first solved each task (defined as consuming food within the tube). We scored only the first 20 min of video footage after the first fish in each group solved each task at which time food items were still visible inside the tube in all trials.

In addition to recording the latency to discovery and solution of the tasks, we also recorded the latency with which each fish entered an arbitrary area (measuring 20 cm x 10 cm) within the tank. This control location contained no food and no distinctive topographical features (such as the wall of the tank). In our analysis, we compared social effects on inter-individual latencies to "discover" the control location with similar latencies to discover the tasks. This comparison allowed us to distinguish social transmission from other processes that might result in a superficially similar pattern of acquisition (see Webster et al. 2013).

7.2.3 Testing for effects of familiarity upon association preferences

We used a randomization test of whether fish preferred to associate with fish from the same habitat background. For each group we constructed a binary habitat matrix indicating whether each pair of fish were from the same habitat (1) or not (0). We then ran a simple regression with the values from the upper triangle of each association matrix as the response, and the upper triangle of the habitat matrix as the predictor. The coefficient of the slope was taken as the test statistic. We generated a null distribution by randomizing the rows and columns within each habitat matrix and recalculating the test statistic 100,000 times. The p-value was taken to be the (1+ number of the null distribution > test statistic)/100,001 (Dekker, Krackhardt&Snijders, 2007; Manly, 2008). Analyses were conducted in the R statistical environment version 2.15.3 (R Core Team, 2013).

7.2.4 Network-based diffusion analysis

To analyse the data we used network based diffusion analysis (NBDA) (Franz and Nunn 2009), specifically the order of acquisition diffusion analysis (OADA) variant (Hoppitt

et al. 2010a). OADA can be used to determine whether the order in which subjects discover and/or solve a task is correlated with different social networks representing different hypotheses about the pathways of transmission. We used the multi-state version of OADA developed by Atton et al. (2012) (Chapter 6 of this thesis), which models multiple options that can be used to solve a task (in this case the two versions of the task) allowing us to distinguish option-specific and cross-option social effects, and teases apart social effects on a) the rate at which fish discover each option; and b) the rate at which fish solve each option once they have discovered it (see Appendix 1 for a full model specification).

We compared the predictive power of three social networks: a) one reflecting observed patterns of association outside of the task context (the "association network") – this represents the hypothesis that the rate of social transmission from individual A to individual B is proportional to the association between them; b) one in which there were binary connections only between individuals from the same diet background (the "familiarity network"– this represents the hypothesis that information is transmitted only between individuals from the same diet background and c) one in which there were binary connections between all the individuals in each group (the "homogeneous network")– this represents the hypothesis that information is transmitted homogeneously between all members of the group (Hoppitt&Laland, 2013). We also fitted a model with different social effects between fish that were familiar and unfamiliar, to allow for the possibility that there was a social effect between all individuals, but that it was stronger between fish that were familiar (Hoppitt and Laland 2013). For each social network we also considered two different models, additive and

multiplicative, for the interaction between social effects and asocial learning (see Hoppitt et al. 2010 for details).

'Holding' and 'group' were included as factors to allow for the possibility that individuals from each of the familiarity holdings, and/or experimental groups might differ systematically in their rates of asocial discovery or solving. We also included factors allowing for an overall bias for the left or right feeder, and an effect of having discovered/solved one option on the rate of discovery/solving the other option. Models were fitted with each combination of network, additive versus multiplicative model, and presence/absence of other factors, excluding group (we considered social effects and group differences in asocial rates of learning as alternative explanations for differences between groups and consequently only included 'group' in models with no social network).

We used a model averaging approach based on Akaike's Information Criterion, corrected for sample size (AICc), to estimate the effects of each predictor variable, accounting for model selection uncertainty, and to quantify the relative support for each network/variable using summed Akaike weights (Burnham & Anderson, 2002; see Appendix 1). Unconditional confidence intervals were calculated using the profile likelihood technique corrected for model selection uncertainty suggested by Burnham & Anderson (2002).

7.3 Results

7.3.1 Effects of familiarity upon association preferences

There was a significant difference in association between fish from the same and different habitat backgrounds (p= 0.001; means: same habitat= 0.366; different habitat= 0.332), though there was considerable variability within each category (Fig. 7.1).
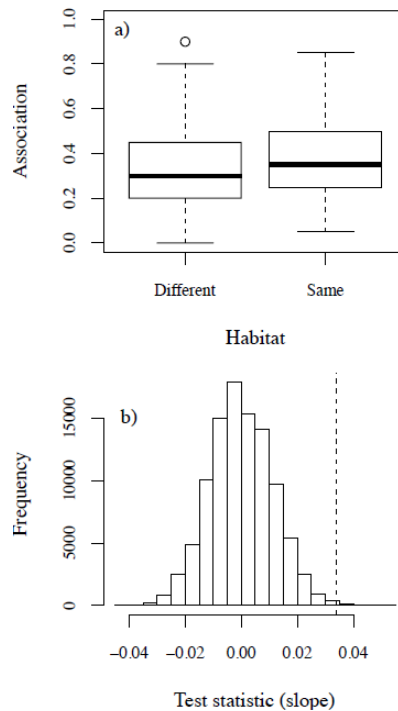
Figure 7.1.(a) Box plot of association strengths familiar and unfamiliar. (b) Histogram showing the null distribution from the randomization test. The dashed line shows the observed test statistic.

7.3.2 Network based diffusion analysis

7.3.2.1 First discovery

There were no trials in which all individuals within a group discovered both options, with the number of discoverers of each option ranging from 0-9. A minimum of 7 individuals discovered one or the other of the options with a total of 60 first discoveries across both individuals and options (see Figure 7.2). Diffusion curves for discovery time (Figure 7.2) generally reveal a rapid increase in number of individuals discovering one option after initial discovery of that same option within the group.
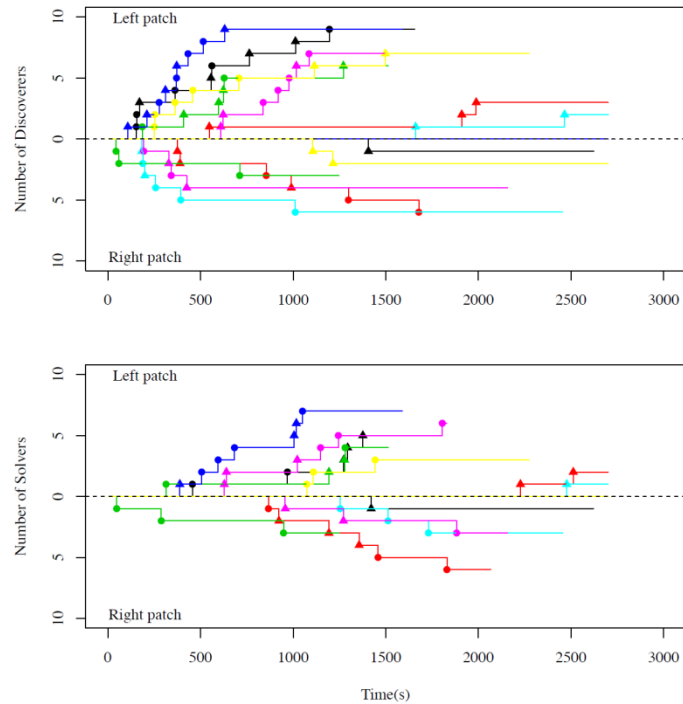
Figure 7.2. The diffusion curves for the times of first discovery (top) and first solving (bottom) showing times for both the left- and right-hand options. Each colour represents a different group. Circles represent individuals fed the Tubifex diet and triangles represent individuals fed the Artemia diet.

7.3.2.2 Support for effect of different social networks on discovery rate

In all seven groups, at least four fish solved a task within the allotted 20 minutes following first solution within a group. No scrounging was observed, as solvers did not move food items outside the tube. There were a total of 39 first solves across all individuals and options.

There was strongest support for the familiarity network influencing on the rate at which individuals discover the tasks (Akaike weight of 86.2% for multiplicative model), with fish being more likely to discover a task if familiar fish have already done so, but not if unfamiliar individuals have discovered the task (see Figure 7.2 & Table 7.1). A homogeneous network receives little support, with an Akaike weight of 5.4%. The association network also receives very little support (Akaike weight = 1.8%), as does a

model with no social effect (Akaike weight= 0.0%). A multiplicative model with the familiarity network was therefore used to estimate the effects reported in *7.3.3.3* below (using model averaging across other predictor variables).

We also fitted a multiplicative model with different social effects between fish from the same (s_{same}) and a different familiarity holding treatment (s_{diff}), allowing us to assess the difference between the two. s_{same} was estimated at 1.80 (95% C.I.= [0.68, 4.52]) and s_{diff} was estimated at 0.20 (95% C.I.= [0, 1.18]), giving an estimated difference of 1.61 (95% C.I.= [0.46, 3.96]), providing evidence of a stronger social effect between familiar individuals. This means the increase in discovery rate for each informed familiar individual relative to the rate of asocial discovery was estimated to be 1.6 units greater than the effect of an informed unfamiliar individual.

Table 7.1. A comparison of the support (based on Akaike weight) for familiarity and homogeneous effects on the discovery of the foraging tasks.

Network	Akaike weight	
No social effect	0.00%	
	Model	
	Additive	**Multiplicative**
SameDiet	5.84%	86.19%
Homogeneous	0.15%	5.42%
Measured	0.60%	1.79%

7.3.2.3 Estimates of effects on discovery rate

Both estimates from the NBDA and support for each variable are shown in Table 7.2. An explanation of the method used to calculate support for each variable (Akaike's Information Criterion) can be found in Chapter 6. There was strong evidence (total

Akaike weight = 100%) that being well connected to familiar individuals who had already discovered an option increased the probability that a naïve individual would be the next to discover that option, providing clear evidence of a social effect on task discovery. The magnitude of this effect was estimated to be a linear increase of 1.5 times (95% CI= [0.64, 3.5]) the average asocial rate of discovery for every informed familiar individual. However, evidence for social transmission of the patch location was unsubstantial, with the contrast between real and control food patches ($s_R - s_C$) estimated at 0.716 (95% CI: [-1.14, 2.75]). The finding that effects of familiarity at real patches were not greater than those at control patches suggests that the social effect on discovery may be a result of associated individuals encountering the task at approximately the same time because of their influence on each other's movements, rather than transmitting the location of the patch once they had discovered it.

There was no evidence that being well-connected to solvers of an option facilitated discovery of that option (over and above their effect as individuals that had discovered that option), and no evidence against an effect of connectedness to discoverers generalising across options (total Akaike weight= 0.0%). There was also little support for the hypothesis that individuals were more likely to discover a option next if they were well connected to individuals who had solved the other task option than if they were not so connected (total Akaike weight= 24.1%). There was little evidence of a difference in the rate of discovery between individuals from each of the familiarity holdings. There was however, strong evidence that individuals that had discovered one option were less likely to discover the other (Akaike weight = 99.8%). There was also strong evidence of a bias toward the left hand task (Akaike weight = 96.2%).

Table 7.2. Two option NBDA results for naïve -> discovered.

Variable	d.f.	Support (sum of Akaike weights)	Model averaged effect estimate	Unconditional 95% confidence interval*
Total network connection to discoverers: option specific	1	100%	1.5	[0.64, 3.5]
Total network connection to discoverers: cross option	1	0%	0	
Total network connection to solvers: option specific	1	0%	0	
Total network connection to solvers: cross option	1	24.1%	0.009	
Holding	1	26.2%	-0.03	
Bias towards left option	1	96.2%	-0.73	[0.23, 1.31]
Group	7	0%	0	
Discovered other option	1	99.8%	-1.67	[-2.78, -0.76]
Solved other option	1	24.2%	0.02	

*Shaded cells indicate there was more support for an effect than against (>50%). Social effects are estimated relative to the mean rate of asocial discovery, e.g. a value of 1.5 signifies that an average individual with one unit of total association to discoverers of an option is 1.5 times faster to discover the same option than an average individual with no connections to discoverers of that option. Unconditional 95% confidence intervals were calculated using a computationally intensive profile likelihood procedure (see Appendix 1) so we only calculated these for variables with support >50%.

7.3.2.4 Support for effect of different social networks on solving rate

There is strongest support for an effect of the familiarity network (Akaike weight:

additive= 35.3%; multiplicative= 28.5%) on the rate at which individuals solve the tasks

(see Table 7.3), with fish being more likely to solve a task if familiar fish have already

done so, but not if unfamiliar individuals have solve the task (Figure 7.2), however this

evidence is not overwhelming: the model with no social effect had an Akaike weight of

8.4%. There was little support for the homogeneous network (Akaike weight: additive

model= 10.0%; multiplicative model= 8.9%) or association network (Akaike weight:

additive model= 4.42%; multiplicative model= 4.38%) suggesting a familiarity-based

social effect is the most likely. The additive familiarity network was used to estimate

the effects below.

Table 7.3: A comparison of the support (based on Akaike weight) for diet-specific and
homogeneous effects on the solving of the foraging tasks.

Network	Akaike weight	
No social effect	8.40%	
	Model	
	Additive	**Multiplicative**
SameDiet	35.29%	28.53%
Homogeneous	10.04%	8.94%
Measured	4.42%	4.38%

7.3.3.5 Estimates of effects on solving rate

As confirmed by the NBDA, diffusion curves for the solving times of the foraging tasks

(Figure 7.2) show individuals solving both options at fairly regular intervals rather than

in collective bursts, suggesting that solvers were not influenced by other solvers. Both estimates from the NBDA and support for each variable are shown in Table 7.4.

There is some suggestive evidence for an option specific effect of solvers (Akaike weight= 70%; s=0.66; 95% CI [0, 3.02]), with individuals being more likely to solve a specific option if they are well connected to previous solvers. However, the evidence is not overwhelming with the unconditional 95% CI including 0. There was little evidence of an effect of familiar fish that had discovered either option, nor of familiar fish that had solved the other option (see Table 7.4).

Table 7.4: Two option NBDA results for discovered non-solver -> solver

Variable	d.f.	Support (sum of Akaike weights)	Model averaged effect estimate	Unconditional 95% confidence interval
Total network connection to discoverers: option specific	1	24.3%	0.05	
Total network connection to discoverers: cross option	1	17.4%	0.03	-
Total network connection to solvers: option specific	1	70%	0.66	[0, 3.02]
Total network connection to solvers: cross option	1	27.3%	0.14	-
Diet	1	25.0%	-0.04	
Bias towards right option	1	27.9%	0.04	
Group	7	3.7%	0.00*	
Discovered other option	1	39.2%	0.22	
Solved other option	1	32.7%	0.30	

* Model averaged estimate of the difference between the fastest and slowest group

7.4 Discussion

Our results provide evidence of an effect of familiarity upon group social organisation, with fish being more likely to associate with familiar than with unfamiliar individuals. Furthermore, familiarity was seen to affect the likelihood of an individual discovering a foraging task, with strong evidence of a social effect on discovery of the foraging tasks, such that individuals tended to discover a task sooner if a familiar individual from their

group had previously done so. Despite finding that familiarity affected both group social structure, and the likelihood of an individual discovering the task, we found that the overall association network of a group had little effect upon the likelihood of an individual discovering a feeding task. In other words, a given fish was no more likely to discover the feeding task if it was strongly connected to fish that had previously discovered it, than it was if it was poorly connected to previous discoverers. Finally, we found no evidence that reduced latency to discovery is a result of task location being socially transmitted between individuals, because the social effect on "discovery" of an empty control patch was plausibly as strong as was discovery of a patch where foraging was possible. The marked similarity in social effects on foraging and control patches suggests that an un-transmitted social effect might underlie the observed diffusions, almost certainly due to the influence of fish on one another's movements.

Such an interpretation is consistent with results of studies of foraging behaviour in stickleback shoals reported in both Chapter 6 (Atton et al. (2012)) and the 'open environment' condition in Webster et al. (2013). In both these studies conducted in open or relatively unstructured environments, similar to the one used in the current study, network structure was a poor predictor of patch discovery (Atton et al. 2012; Webster et al. 2013). In contrast, in structurally complex environments, order of patch discovery was linked to network structure (Webster et al. 2013). This difference in outcome may be due to the effects of the environment upon network characteristics, as groups in structurally complex environments had lower network density overall, and more heterogenous, 'cliquey' networks than groups in structurally simple environments. Difference in outcome may also be due to structured environments limiting the distance over which social cues indicative of patch location, such as feeding behaviours, can be detected, making it more likely that only closely associating individuals will detect cues

containing foraging information from one another (Atton et al. 2012; Webster et al. 2013).

In addition to influencing task discovery, familiarity was also seen to have an effect upon latency to solve the feeding tasks, with individuals being more likely to solve a task when familiar than when unfamiliar individuals had already done so. Evidence of a difference in the effects of familiar and unfamiliar individuals on task solution is not particularly strong. However, the familiarity network explains the data better than does a homogeneous network, suggesting a familiarity-based social effect is present. Such an interpretation is consistent with the social effects seen in the same model, where there was also some support for an effect on the rate of an individual solving a specific task when they were well connected to familiar previous solvers.

Finding an effect of familiarity on task solution is consistent with the results of previous studies, that have found that associations between familiar individuals can give rise to directed social transmission of information (Lachlan et al. 1998; Swaney et al. 2001). If so, shoaling with familiar fish may be adaptive, in that it may allow individuals to locate resources more rapidly or with greater efficiency when foraging with familiar than unfamiliar group mates. Shoaling with familiar individuals has also been suggested to provide anti-predator benefits in some species through greater shoal cohesion (Chivers et al. 1995).

The mechanism underlying familiarity effects on information acquisition is not clear. Familiarity effects may reflect a perceptual or attentional bias for observing or more strongly responding to the behaviour of familiar individuals. Where familiarity is based upon diet- or habitat-derived cues, selection might favour behaviour whereby individuals follow or copy others that are exploiting the same range of resources (Ward

et al. 2007; Webster et al. 2009b). A tendency to follow or copy the behaviour of individuals exploiting similar resources may also occur when familiarity is based solely upon learned recognition, because the development of learned recognition requires prolonged interaction that may also result in individuals being exposed to and exploiting similar resources. Our methods allowed both learned and resource-derived familiarity to develop within our treatment subgroups. Useful further work might seek to determine the relative contributions of these two forms of recognition to the effects observed in the current study and to identify the way in which each increases the likelihood of patch discovery.

7.5 Summary

In summary, familiarity between shoal members had a clear effect on discovery of prey patches. Familiarity was also seen, to a lesser extent, to affect solving of a novel foraging task. These results demonstrate that factors that affect fine-scale social interactions can influence how individuals encounter and exploit resources, and suggests that researchers should take into account such social factors when investigating how information and behaviour diffuse through populations.

Chapter 8. General discussion

8.1 Overall objective

Due to its small size, wide geographical distribution and ease of retaining in the laboratory, the threespined stickleback is an excellent species in which to study social learning and transmission, and indeed is used as a model species throughout biology. It is particularly effective for investigating the transmission of information through populations, and how social network structure affects that diffusion, since it is relatively straight forward and cheap to establish replicate populations in the laboratory. There are a number of studies which provide evidence that both threespined and ninespined sticklebacks possess the ability to learn socially under a range of contexts, such as foraging, anti-predator behaviour, mate choice, and cooperation. The studies presented in this thesis extend these and shed light on the mechanisms.

The objective of the experiments contained within this thesis was to provide further insight into the social learning capabilities of threespined sticklebacks and build upon present knowledge with regards to the social learning processes used by the species, the contexts under which they are used, and the factors affecting the transmission of information through populations. In all these respects, the experiments have been successful.

8.2 Social learning processes

The ability to learn socially can prove advantageous in a dynamic environment, aiding in the gathering of relevant and up to date information in order to make informed, biologically important decisions, which in turn can affect survival and reproduction. There are many different processes by which social learning can occur, including

imitation, goal emulation, observational conditioning, local enhancement, stimulus enhancement, social facilitation, response facilitation, observational R-S learning, and the social enhancement of food preferences. Evidence for some, but not others, of these processes is reported in this thesis.

8.2.1 Social learning processes studied and identified

8.2.1.1 Delayed local enhancement

The first experiment, presented in Chapter 3 of this thesis, tested both threespined and ninespined sticklebacks in their use of the social learning process of delayed local enhancement to select a shelter that previously housed a small shoal of conspecifics. Both species were shown to elicit a preference to be in the vicinity of the demonstrated shelter whilst it contained the demonstrator shoal during the demonstration phase. However, neither threespined nor ninespined sticklebacks showed a significant preference for the previously demonstrated end of the tank during the test phase. Previous studies (e.g. Coolen et al 2003) however, have indentified the use of the social learning process of delayed local enhancement in both species, implying that the absence of its use in this instance can be explained by the difference in context under which its use was examined (discussed further in section 8.3.1.1). Nonetheless, it is perhaps surprising that these fishes should possess the psychological capability for a particular social learning mechanism, but not deploy it in a context where it would be ostensibly valuable.

8.2.1.2 The social enhancement of food preferences

The experiment in Chapter 4 explores the social learning process of the social enhancement of food preferences. However, rather than enhancing a preference for a particular food, it was shown that threespined sticklebacks will avoid the diet of stressed

conspecifics. In circumstances where demonstrator animals exhibit signs of stress, it is logical to assume that avoiding performance of their behaviour may be adaptive. While there is extensive evidence amongst animals for the social transmission of information through which the observer and demonstrator come to exhibit the same behaviour, it is comparatively rare for animals to learn from conspecifics what not to do.

Previous work of mine (Atton 2010) had established that when given a choice between two novel foods, rather than display a preference for the demonstrated food, as seen in Norway rats (Galef 1983; Galef and Wigmore 1983; Galef 1988; Galef 2005), threespined sticklebacks showed no preference for either food type under normal laboratory conditions, but displayed a preference for the non-demonstrated food type when both demonstrators and observer were under stress. I extended this work in Chapter 4 by changing the base colour of the tank between stages 2 and 3 of the experiment (stage 2 being the hour directly after the demonstrators had fed and stage 3 being the hour for which the observer was introduced to the demonstrators). In this way it was possible to distinguish that the negative association seen previously by Atton (2010) was a result of the observers receiving stress cues from the demonstrators alongside the prey-specific cues being excreted in the urine or epidermal mucus of the demonstrators that allowed the observers to develop a negative association to the demonstrated food. These findings thereby establish a novel mechanism for the avoidance of maladaptive information transmission in fishes. By avoiding food types associated with conspecific stress cues, an individual may avoid ingesting potentially harmful substances, or avoid foraging for a specific prey type that is only found in areas of high predation risk.

8.2.1.3. Local enhancement

In Chapters 6 and 7, shoals of threespined sticklebacks were presented with two identical foraging tasks and network-based diffusion analysis (NBDA) was applied to determine whether the order in which individuals in a social group discovered and solved the tasks was affected by the group's network structure. The use of NBDA allowed for a more detailed investigation of mechanisms, which established that social transmission could be ruled out, where it might otherwise have been assumed.

There was strong evidence in both chapters for a social effect on discovery of the foraging tasks, with individuals tending to discover a task sooner when others in their group had previously done so. However, the same patterns of association did not reliably predict the spread of the solution to the tasks, suggesting that social interactions affected the time at which the tasks were discovered, but not the latency to its solution following discovery.

In both instances, we find no evidence that this effect is the result of the task location being socially transmitted between individuals, since the social effect on "discovery" of an arbitrary empty control patch appeared as strong as the discovery of a patch where foraging was possible. These findings suggest that an untransmitted social effect underlies the observed diffusions - almost certainly the influence of fish on one another's movements. There is evidence for the social learning process of local enhancement in both experiments, but in neither case does this support social transmission.

Chapters 6 and 7 illustrate how NBDA can lead to insight into the mechanisms supporting behaviour acquisition that more conventional statistical approaches might miss. Importantly, they also provide compelling evidence that the spread of novel

behaviours can result from social learning in the absence of social transmission, an untransmitted social effect on learning. There are a number of previous studies of social learning in fish that report social effects consistent with the hypothesis of a mutually reinforcing tendency of individuals that have discovered a potential food source to remain near that food source and eventually learn to exploit it (eg. Baird et al. 1991; Laland and Williams 1997; Day et al. 2001; Webster and Hart 2006). The present findings are of particular significance in that they draw attention to the possibility that many natural diffusions may similarly result from untransmitted social effects, rather than from either social transmission or asocial learning as frequently reported.

8.2.1.4 Stimulus enhancement

The social learning process of stimulus enhancement however, was identified as a possible explanation for some of the results seen in chapter 6. Unexpectedly, in the two-task experiment, we found that associating with others that have previously solved one option leads to an increased rate of discovery of the remaining option. Because the two tasks were identical, stimulus enhancement of one task may have led to increased attention to the other. Given the surprising absence of clear evidence for stimiulus enhancement in animals (Hoppitt & Laland 2008, 2013), this finding is of some significance.

8.3 Contexts under which social learning is used

There is a host of evidence to suggest that fish have the capability to utilise social learning processes and strategies under a variety of contexts, including mate choice copying, migration and orientation, foraging, anti-predator behaviour, and aggressive interactions. The experiments in this thesis focused on a foraging context with the exception of chapter 3, which looked at the context of shelter choice.

8.3.1 Contexts studied

8.3.1.1 Shelter choice

As discussed previously, both threespined sticklebacks and ninespined sticklebacks were shown to elicit a preference to be in the vicinity of the demonstrated shelter whilst it contained the demonstrator shoal during the demonstration phase in the experiment conducted in Chapter 3. However, neither threespined nor ninespined sticklebacks showed a significant preference for the previously demonstrated end of the tank during the test phase, suggesting that neither species used delayed local enhancement to influence shelter choice, despite evidence of both species being able to utilise this social learning process under a foraging context (Coolen et al. 2003). It is therefore apparent that the use of this social learning process is context specific. This may be due to the fact that adequate shelter is likely to be more readily available and easier to locate than profitable foraging patches, therefore the adaptation of using delayed local enhancement to locate shelter is not sufficiently advantageous to be readily employed under a shelter choice context.

8.3.1.2 Foraging

The remaining experiments (Chapters 4 – 7) all took place under a foraging context and provide significant evidence that social learning impacts upon the foraging decisions of sticklebacks in a number of ways. For example, social learning facilitates locating food, as seen in Chapters 6 and 7, and provides information on which food type is to be consumed, as seen in Chapter 4.

It is apparent from Chapter 4 that threespined sticklebacks are able to detect and identify a specific food type that has been eaten by conspecifics, possibly via amino acids excreted in the urine and that they subsequently avoid this food type if the conspecifics

that had recently consumed it are displaying signs of stress. The experiment in Chapter 7 then went on to show that threespined sticklebacks are also able to identify prey types consumed by others and use this information with regards to self-referent matching, identifying individuals that have consumed the same prey type as themselves, and in turn be more influenced by them in their actions and in this case, increasing their chances of discovering a food source. In both cases, social information is being exploited in a manner that potentially enhances the effectiveness of individual decision making, thereby incrementing fitness.

8.4   Impacts of the social network

With networks now being recognised as present at a variety of biological levels, the study of network theory has been utilised widely by biologists (Croft et al. 2008). Included in this is the study of the social network structure of a group or population. A non-random network structure can be generated by variety of different phenotypic factors and the use of network theory provides a number of useful metrics for quantifying this social structure. The study of animal social networks also has the potential to provide us with a wealth of previously inaccessible knowledge concerning the behaviour of animals under a wide variety of contexts including cooperation, disease transmission, social structure, and the role of individuals Krause et al. 2007)

The last two experiments in this thesis, Chapters 6 and 7, focused upon identifying potential effects of the social network on the transmission of information through a population under a foraging context. As discussed above, populations of threespined sticklebacks were presented with two identical foraging tasks and NBDA was applied to determine whether the order in which individuals in a social group discovered and

solved the tasks was affected by the group's network structure. Even though NBDA showed an untransmitted social effect, it was still apparent in Chapter 6 that the spread of discovery of the foraging tasks was influenced by groups' social networks, with individuals being more likely to discover a task when others they were more closely associated with had previously done so. The social network of a population can therefore be said to influence an individual's foraging success, dependent upon with whom they form an association.

In Chapter 7, shoals of threespined sticklebacks consisted of an equal ratio of fish fed on one of two diets. Familiarity between shoal members had a clear effect on discovery of prey patches. Familiarity was also seen, to a lesser extent, to affect solving of a novel foraging task. These results demonstrate that factors that affect fine-scale social interactions can influence how individuals encounter and exploit resources, and suggests that researchers should take into account such social factors when investigating how information and behaviour diffuse through populations.

8.5   Future studies

8.5.1 Avoidance of maladaptive information transmission

The findings from Chapter 4 establish a novel mechanism for the avoidance of maladaptive information transmission in fishes, with threespined sticklebacks being shown to avoid a novel food when that food is associated with the stress cues of conspecifics. This is a very interesting finding, as while there is extensive evidence amongst animals for the social transmission of information through which the observer and demonstrator come to exhibit the same behaviour, it is comparatively rare for animals to learn from conspecifics what not to do, leading observing animals to perform

different, or opposite, behaviour from their demonstrators. However, in circumstances where demonstrator animals exhibit signs of stress, avoiding performance of their behaviour may be adaptive.

It would therefore be beneficial to expand upon this study by searching for this mechanism in different species and under different contexts. One such study would be a species comparison between threespined sticklebacks and ninespined sticklebacks. Differences in the use of social learning mechanisms between these two closely related species have already shown to be apparent, with ninespined sticklebacks having been shown to be able to utilise public information under a foraging context whilst threespines do not (Coolen et al. 2003, 2005). It would therefore be interesting to examine whether or not they differ further in other adaptive foraging mechanisms. Ninespined sticklebacks have also been shown to utilise public foraging information from both conspecifics and heterospecific threespines (Coolen et al. 2003, 2005). It is possible that the avoidance of maladaptive information may also be utilised with information from heterospecifics. A further study could therefore be undertaken using threespined focal individuals and heterospecific ninespined demonstrators and vice versa.

It is also plausible that this mechanism may be widespread in teleost fishes where there are social influences on foraging and could be tested for in a variety of species, which may provide insight into the evolution of the process.

8.5.2 Self-referent matching or familiarity?

Due to the nature of the experimental setup in Chapter 7, it was not possible to distinguish whether the observed effect of individuals from one diet group being more likely to discover a food source when an individual of the same diet had previously

done so was due to self-referent matching, as assumed, or familiarity. For example, Griffiths and Magurran (1997a) have shown that guppies have the capability to recognise and become familiar with up to 40 other individuals, similar to the number of threespined sticklebacks that were assigned to each diet background and cohabited. It is possible that threespined sticklebacks share this ability and that the strategy they adhered to was *copy-the-familiar,* rather than being an effect of self-referent matching to diet and/or habitat cues. Further studies will need to be carried out to tease apart these two possible mechanisms.

This can be done repeating the experiment, but this time housing the fish in 10 separate groups of 7 fish (the number of groups would be dependent upon the number of trials). 5 of the groups would be fed diet A and the other 5 groups diet B. The test populations would then be made up of 1 fish from each group, resulting in 5 unfamiliar fish sharing each diet.

8.5.3 Additional phenotypic factors affecting the discovery of a food source

In Chapter 6 the phenotype of each study population was manipulated by varying the size of fish, with equal numbers of 'large' and 'small' fish being present in each group. Size was not shown to have any impact upon the social network of each population, or upon the likelihood of discovering the foraging task(s). In Chapter 7 the phenotype of each group was manipulated by diet and/or familiarity, with equal numbers of fish in each population being housed separately and fed on one of two diets prior to each trial. Whilst this difference in diet and/or familiarity was shown not to have an effect upon the social network, it did however, significantly affect the likelihood of an individual discovering the foraging tasks, with fish of the same diet being more likely to discover the task in succession.

Further studies can be undertaken to establish additional aspects of phenotypes that may affect the order in which a food source is discovered. Such a study could be based upon social learning strategies, with particular attention paid to 'who' strategies.

Populations of threespined sticklebacks could be manipulated with regards to a *copy-successful-individuals* strategy. This could be carried with regards to either hunger state or health, for example by creating populations containing recently fed and starved individuals, or by using populations containing parasitised and non-parastised individuals. It could be hypothesised that 'unsuccessful' individuals may be more likely to discover a food source when observing a 'successful' individual who has discovered it previously than a less successful individual. Likewise *copy-kin* is also a plausible investigation that could be undertaken using the same experimental setup, with populations being comprised of groups of related or unrelated individuals.

It would also be interesting to carry out the same experiments using ninespined sticklebacks, however, there would be technical difficulties with regards to tagging the fish for individual identification, as the dorsal spines on the ninespined sticklebacks are significantly smaller than those of the threespines.

8.6   Conclusions

In sum, in this thesis I set out to provide further insight into the social learning capabilities of threespined sticklebacks. I found that a variety of social learning processes are used under the context of foraging, and that the use of these processes is affected by a number of phenotypic factors and the social network of a population.

Appendix 1

Supplementary Material for Chapter 6

1.TADA and OADA

Both TADA and OADA variants of NBDA can be expressed, for multiple diffusions in different groups, as either:

$$\lambda_{ik}(t) = \lambda_{0k}(t)\big(1 - z_{ik}(t)\big)\left(s \sum_{j=1}^{N_k} a_{ijk} z_{jk}(t) + exp(\psi_{ik}) \right)$$

Eqn. S1a

In which the rate of social transmission and asocial learning combine additively, or a multiplicative model:

$$\lambda_{ik}(t) = \lambda_{0k}(t)\big(1 - z_{ik}(t)\big)\left(s \sum_{j=1}^{N_k} a_{ijk} z_{jk}(t) + 1 \right) exp(\psi_{ik})$$

Eqn. S1b

Where:

$\lambda_{ik}(t)$ is the rate of acquisition (or "hazard rate" in survival analysis terminology) of the trait for individual *i* in group *k* at time *t;*

$\lambda_{0k}(t)$ is a baseline rate function for individuals in group *k*;

$z_{ik}(t)$ is an indicator variable giving the status of *i* in group *k* at time *t* (1= informed; 0=naïve);

a_{ijk} is the network connection from *j* to *i* in group *k*;

s is a parameter giving the strength of social learning (≥ 0; but see section 3, below); and

ψ_{ik} is a linear predictor allowing the modelling of the effect of individual level variables (e.g. size) in a manner analogous to a Cox survival model or generalised linear model (GLM); and

N_k is the number of individuals in group *k*.

The original TADA (Franz and Nunn, 2009) assumes that $\lambda_{0k}(t) = \lambda_0$, i.e. a constant, but Hoppitt et al. (2010b) found that this assumption could lead to false positives if $\lambda_{0k}(t)$ was systematically increasing. This problem can be alleviated if a suitable function can be found to model $\lambda_{0k}(t)$. OADA, in contrast, makes no assumptions about the shape of $\lambda_{0k}(t)$, and should therefore be used if a suitable model is not available for $\lambda_{0k}(t)$ (Hoppitt & Laland, 2011). We decided to use OADA since it makes fewer assumptions about the baseline acquisition function, though modified as described in section 2.

Hoppitt et al (2010a) suggested that the multiplicative model might be more appropriate for indirect social influences on learning, such as local enhancement(which, in the Discussion we suggest to be responsible for some of the observed social effects) and the additive model more appropriate for processes that directly result in social learning. Hoppitt et al suggest using the relative fit of the additive and multiplicative models to distinguish between direct and indirect social influences. However, in a simulation study (Hoppitt, unpublished) we found that there was little if any distinguishing power. Furthermore, it seems intuitively obvious that the multiplicative model will fit better if individual level variables influence both asocial and social learning ability in the same way, even if social transmission is aseparate stochastic process. Consequently, we do not attempt to use the additive and multiplicative models to distinguish social learning mechanism in the way suggested by Hoppitt et al (2010a).

2. Modifying OADA for multiple groups

The form of OADA for multiple diffusions given by Hoppitt et al (2010a) is only sensitive to the order of acquisition within groups, and so is not sensitive to between group patterns (see main text), i.e. it allows for a different $\lambda_{0k}(t)$ for each group. However, we felt it was reasonable to assume that there is a common baseline rate function for all groups $\lambda_{0k}(t) = \lambda_0(t)$, since groups were selected from the same population and diffusions run in identical and constant laboratory conditions. We accomplished this by treating the data the order across groups,

effectively as a single diffusion, but with zero social network connections between individuals in different groups. We did, however, allow for a proportional difference in the rate of discovery and solving in each group at any given time, which was considered as an alternative explanation to social transmission. This was accomplished by including "group" as a factor in the linear predictor ψ_{ik}. We then ran additional analyses to determine whether social effects followed the social network or whether they operated homogeneously across each group.

3. Three state NBDA

We applied this multistate version of NBDA to the data from a single task experiment, the results of which are reported in section 8 below. The model was further expanded to allow for two options (tasks), as reported in section 6 below. We expanded NBDA from a two state model (naïve->informed) to a three state model (naïve-> discovered non-solver -> solver), which allowed us to examine the social effects on each transition. Analysing the rate of discovery (naïve->discovered) and solving (naïve -> solver) separately (e.g. Hoppitt et al 2010a) fails to fully tease apart the two transitions. The additive model for discovery is expressed generally as follows:

$$\lambda_{D,ik}(t) = \lambda_{D,0k}(t)\big(1 - d_{ik}(t)\big)\left(s_{DD} \sum_{j=1}^{N_k} a_{ijk}d_{jk}(t) + s_{DS} \sum_{j=1}^{N_k} a_{ijk}z_{jk}(t) + exp\big(\psi_{D,ik}\big) \right)$$

Eqn. S2a

And the multiplicative as:

$$\lambda_{D,ik}(t) = \lambda_{D,0k}(t)\big(1 - d_{ik}(t)\big)\left(s_{DD} \sum_{j=1}^{N_k} a_{ijk}d_{jk}(t) + s_{DS} \sum_{j=1}^{N_k} a_{ijk}z_{jk}(t) + 1 \right)exp\big(\psi_{D,ik}\big)$$

Eqn. S2b

Where:

$\lambda_{D,ik}(t)$ is the rate of discovery and $\lambda_{D,0k}(t)$ the corresponding baseline function, taken here to be $\lambda_{D,0k}(t) = \lambda_{D,0}(t)$, see section 2;

$z_{ik}(t)$ remains an indicator for whether *i* in group *k* has solved the task prior to time *t*; whereas $d_{ik}(t)$ is an indicator for whether *i* in group *k* has discovered the task prior to time *t*, regardless of whether *i* has yet solved the task;

s_{DD} is then a parameter giving the social effect of connected individuals who have discovered the task on rate of discovery;

s_{DS} is then a parameter giving the additional social effect of connected individuals who have also solved the task on rate of discovery; and

$\psi_{D,ik}$ is a linear predictor as above.

The additive model for solving is then:

$$\lambda_{S,ik}(t) = \lambda_{S,0k}(t)\big(d_{ik}(t) - z_{ik}(t)\big)\left(s_{SD} \sum_{j=1}^{N_k} a_{ijk}d_{jk}(t) + s_{SS} \sum_{j=1}^{N_k} a_{ijk}z_{jk}(t) + exp\big(\psi_{S,ik}\big) \right)$$

Eqn. S3a

And the multiplicative is

$$\lambda_{S,ik}(t) = \lambda_{S,0k}(t)\big(d_{ik}(t) - z_{ik}(t)\big)\left(s_{SD} \sum_{j=1}^{N_k} a_{ijk}d_{jk}(t) + s_{SS} \sum_{j=1}^{N_k} a_{ijk}z_{jk}(t) + 1 \right) exp\big(\psi_{S,ik}\big)$$

Eqn. S3b

$\lambda_{S,ik}(t)$ is the rate of solving for discovered individuals and $\lambda_{S,0k}(t)$ the corresponding baseline function, taken here to be $\lambda_{S,0k}(t) = \lambda_{S,0}(t)$, see section 2;

s_{SD} is then a parameter giving the social effect of connected individuals who have discovered the task on rate of solving; and

s_{SS} is then a parameter giving the additional social effect of connected individuals who have also solved the task on rate of solving; and

$\psi_{S,ik}$ is a linear predictor as above.

Note the $\big(d_{ik}(t) - z_{ik}(t)\big)$ term ensures that only individuals who have discovered the task $(d_{ik}(t) = 1)$ but not solved it $(z_{ik}(t) = 0)$, are included in the likelihood function for a given solving event occurring at time t.

For all NBDA models, we suggest that individual-level variables included in the linear predictor,

$\psi_{D,ik}$, are transformed by subtracting the mean across all individuals. This means that the

social effects can be interpreted consistently as the increase in rate per unit of network

connection, relative to the average asocial rate.

We calculated the likelihood function in an analogous manner to the standard OADA (see

Hoppitt et al 2010a) or Cox model (Therneau&Grambsch 2000). We used the "exact" method

to correct for ties which sums the log-likelihood across all orders that are consistent with the data(Hoppitt et al 2010a, Therneau&Grambsch 2000). Models were fitted using maximum likelihood using the nlminb or optim optimisation functions in the R 2.11.1 statistical environment (R Development Core Team 2010).TADA using discrete (Franz & Nunn 2009) or continuous (Hoppitt et al 2010a) data could also be used to fit the three state model (and two option model below) if suitable baseline rate functions,$\lambda_{D,0k}(t)$ and $\lambda_{S,0k}(t)$can be found (Hoppitt et al 2010b).

Hoppitt et al (2010a) suggest reporting a more intuitive parameterisation in which the parameter giving the strength of social transmission is bounded between 0 (no social transmission) and 1 (all social transmission). It is possible to parameterise the multi-state models here such that there is a single such parameter representing the overall importance of social learning for each transition, with other parameters giving the relative effect of different types of individual (e.g. solvers versus demonstrators). However, we found the models were difficult to fit in this parameterisation, meaning we could not get confidence intervals using the methods described in section 4 below. Consequently we use the unbounded parameterisation here.

4. Model averaging and unconditional confidence intervals

Before calculating model-averaged estimates, we dropped any models in which the fitted value for any parameter was zero, since this would result in model redundancy (Burnham & Anderson 2002). We calculated model-averaged estimates for each parameter using the procedure given in Burnham and Anderson (2002). We performed model averaging across additive social transmission models and models without social transmission, since the additive model was favoured. It makes little sense to average across additive and multiplicative models since the s parameters operate on different functions. In every case we calculated across the

entire set of such models, since, where are parameter was not present it could be interpreted as having a value of zero (Burnham & Anderson 2002).

Burnham and Anderson (2002) present a method for calculating unconditional standard errors for parameters that allows for model uncertainty, which can be used to calculate unconditional Wald confidence intervals. However, we found this method to be misleading since standard errors only reflect the local shape of the likelihood function at the maximum likelihood estimator (MLE), and so Wald confidence intervals can be misleading where the likelihood surface if asymmetrical about the MLE. This is the case for many of our parameters.

95% confidence intervals can also be constructed using profile likelihood techniques (Morgan 2009), which involves determining the set of values for a parameter, θ, that could not be rejected at the 5% level in a likelihood ratio test (LRT) against a model in which θ is unconstrained. This gives a more accurate picture when the likelihood surface is asymmetrical. Burnham and Anderson (2002) propose a method for adjusting profile likelihood confidence intervals by increasing the critical value for rejection in the LRT, based on the unconditional standard error. We calculated profile likelihoods from the best K-L model and used obtained conditional standard errors for each model from the numerical estimate of the Hessian matrix, returned by the optim function.

5 Two option NBDA

The full additive models for the two-option extension are:

$$\lambda_{D,ik1}(t) = \lambda_{D,0k}(t)\big(1 - d_{ik1}(t)\big)\Bigg(s_{DD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t)$$

$$+ s_{DS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t) + s_{DD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t) + s_{DS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t)$$

$$+ exp\Big(\psi_{D,ik} + \alpha d_{jk2}(t) + \beta z_{jk2}(t)\Big)\Bigg)$$

Eqn. S5a

$$\lambda_{D,ik2}(t) = \lambda_{D,0k}(t)\big(1 - d_{ik2}(t)\big)\Bigg(s_{DD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t)$$

$$+ s_{DS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t) + s_{DD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t) + s_{DS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t)$$

$$+ exp\Big(\psi_{D,ik} + \alpha d_{jk1}(t) + \beta z_{jk1}(t)\Big)\Bigg)$$

Eqn. S5b

$$\lambda_{S,ik1}(t) = \lambda_{S,0k}(t)\big(d_{ik1}(t) - z_{ik1}(t)\big)\Bigg(s_{SD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t)$$

$$+ s_{SS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t) + s_{SD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t) + s_{SS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t)$$

$$+ exp\Big(\psi_{S,ik} + \gamma d_{jk2}(t) + \delta z_{jk2}(t)\Big)\Bigg)$$

Eqn. S5c

$$\lambda_{S,ik2}(t) = \lambda_{S,0k}(t)\big(d_{ik2}(t) - z_{ik2}(t)\big)\left(s_{SD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t) \right.$$

$$+ s_{SS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t) + s_{SD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t) + s_{SS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t)$$

$$\left. + exp\big(\psi_{S,ik} + \gamma d_{jk1}(t) + \delta z_{jk1}(t)\big) \right)$$

Eqn. S5d

where:

$\lambda_{D,ikm}(t)$ is the rate of discovery of option *m* by *i* in group *k* at time *t*;

$\lambda_{S,ikm}(t)$ is the rate of solving of option *m* by *i* in group *k* at time *t*;

$z_{jkm}(t)$ is an indicator for whether *i* in group *k* has solved the task using option *m* prior to time *t*;

$d_{ikm}(t)$ is an indicator for whether *i* in group *k* has discovered option *m* prior to time *t*, regardless of whether *i* has yet solved the task using option *m*;

On s parameters, the subscript *OS* indicates that a social effect is option specific, whereas *CO* indicates that it operates across options ("cross option").

α is the effect on discovery rate of option *m*, on the scale of the linear predictor, of having previously discovered the other option;

β is the effect on discovery rate of option *m*, on the scale of the linear predictor, of having previously solved the other option;

γ is the effect on discovery rate of option *m*, on the scale of the linear predictor, of having previously discovered the other option;

δ is the effect on discovery rate of option *m*, on the scale of the linear predictor, of having previously solved the other option.

Note the common baseline rate functions across options, $\lambda_{D,0k}(t)$ and $\lambda_{S,0k}(t)$, taken to be $\lambda_{D,0}(t)$ and $\lambda_{S,0}(t)$ respectively (the same shape across groups). This means that the model for discovery takes as data the order of discovery across groups and options, and the model for solving takes as data the order of solving across groups and options. The $\big(d_{ikm}(t) - z_{ikm}(t)\big)$ term ensures individuals are only included in the likelihood function for a solving event at time *t* for options they have discovered, $(d_{ikm}(t) = 1)$ but not solved $(z_{ikm}(t) = 0)$.

We calculated the likelihood function in an analogous manner to the standard OADA (see Hoppitt et al 2010a) or Cox model (Therneau&Grambsch 2000). We used the "exact" method to correct for ties which sums the log-likelihood across all orders that are consistent with the data (Hoppitt et al 2010a, Therneau&Grambsch 2000). Models were fitted using maximum likelihood using the nlminb or optim optimisation functions in the R 2.11.1 statistical environment (R Development Core Team 2010).

The full multiplicative models are given by:

$$\lambda_{D,ik1}(t) = \lambda_{D,0k}(t)\big(1 - d_{ik1}(t)\big)\Bigg(s_{DD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t)$$

$$+ s_{DS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t) + s_{DD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t) + s_{DS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t)$$

$$+ 1 \Bigg) exp\Big(\psi_{D,ik} + \alpha d_{jk2}(t) + \beta z_{jk2}(t)\Big)$$

Eqn. S6a

$$\lambda_{D,ik2}(t) = \lambda_{D,0k}(t)\big(1 - d_{ik2}(t)\big)\Bigg(s_{DD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t)$$

$$+ s_{DS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t) + s_{DD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t) + s_{DS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t)$$

$$+ 1 \Bigg) exp\Big(\psi_{D,ik} + \alpha d_{jk1}(t) + \beta z_{jk1}(t)\Big)$$

Eqn. S6b

$$\lambda_{S,ik1}(t) = \lambda_{S,0k}(t)\big(d_{ik1}(t) - z_{ik1}(t)\big)\Bigg(s_{SD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t)$$

$$+ s_{SS,OS} \sum_{j=1}^{N_k} a_{ijk} z_{jk1}(t) + s_{SD,CO} \sum_{j=1}^{N_k} a_{ijk} d_{jk2}(t) + s_{SS,CO} \sum_{j=1}^{N_k} a_{ijk} z_{jk2}(t)$$

$$+ 1 \Bigg) exp\Big(\psi_{S,ik} + \gamma d_{jk2}(t) + \delta z_{jk2}(t)\Big)$$

Eqn. S6c

$$\lambda_{S,ik2}(t) = \lambda_{S,0k}(t)\big(d_{ik2}(t) - z_{ik2}(t)\big)\left(s_{SD,OS} \sum_{j=1}^{N_k} a_{ijk}d_{jk2}(t) \right.$$

$$+ s_{SS,OS} \sum_{j=1}^{N_k} a_{ijk}z_{jk2}(t) + s_{SD,CO} \sum_{j=1}^{N_k} a_{ijk}d_{jk1}(t) + s_{SS,CO} \sum_{j=1}^{N_k} a_{ijk}z_{jk1}(t)$$

$$\left. + 1 \right) exp\left(\psi_{S,ik} + \gamma d_{jk1}(t) + \delta z_{jk1}(t) \right)$$

Eqn. S6d

6 Models fitted for two-task experiment

File 2TaskDiscoveryModels.txt gives the list of models fitted for the two-task experiment to the rate of discovery transition. File 2TaskSolvingModels.txt gives the list of models fitted for the two-task experiment to the rate of solving transition. Both are in tab delimited text format.

The maximum likelihood estimators are given: where NA indicates a variable was not included in a model. The standard errors are also given, calculated from the numerical estimate of the Hessian matrix provided by the optima function.

7 Homogeneous versus network-specific effects

As explained above, the OADA used here is sensitive to between-group differences in discovery and solving times. Consequently, evidence of an effect of network connections to other 'discovered' and/or 'solved' individuals might reflect an effect that operates homogeneously amongall individuals in each group, rather than following the social network. To tease apart which effect was operating, we fitted alternative versions of models for rate of discovery/solving. To reduce the set of models to be fitted, we constrained all models to include the effects for which there was more support for than against (>50%). To assess whether each social effect operated homogeneously between groups, we replaced the social network based with a homogeneous network (connection of strength 1 for individuals in the same group, 0 for those in a different group) for each effect. We also allowed for the

possibility of network-specific and homogeneous components to each effect (see below). We considered both additive and multiplicative models. We calculated the total support for a network-specific component for each social effect by summing the Akaike weights for the models in which it was present. If such support were strong, it would suggest that the strength of connections to other individuals is important, as oppose to the number of individuals in a specific state in the same group.

To assess the evidence for whether each social effect operated via the social network within groups, or whether it operated with equal strength between all individuals in a group, we fit alternative models in which the social network was replaced with a network that was homogeneous within groups. For example, for the option specific effect of total connection to discoverers, on the rate of discovery, we replaced

$$s_{DD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t)$$

Eqn. S7a

with

$$\acute{s}_{DD,OS} \sum_{j=1}^{N_k} d_{jk1}(t)$$

Eqn. S7b

Equivalent to setting all $a_{ijk} = 1$. We also allowed for the fact that a social effect might have network specific and homogeneous component, in which case we instead used the term:

$$\acute{s}_{DD,OS} \sum_{j=1}^{N_k} d_{jk1}(t) + s_{DD,OS} \sum_{j=1}^{N_k} a_{ijk} d_{jk1}(t)$$

Eqn. S7c

Here, the rate of social transmission is linearly related to network connection strength with slope $s_{DD,OS}$ and intercept $\acute{s}_{DD,OS}$.

References

Akins, C. K., and Zentall, T. R. (1996), Imitative learning in male Japanese quail (*Coturnix japonica*) using the two action method, *Journal of Comparative Pyschology,* 110: 316–320.

Allen, J., Weinrich, M., Hoppitt, W., and Rendell, L. (2013), Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales, *Science*, 340: 485-488.

Anthouard, M. (1987), A study of social transmission in juvenile *Dicentrarchus labrax* (Pisces, Serranidae), in an operant-conditioning situation, *Behaviour,* 103: 266-275.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., and Sheldon, B. C. (2012), Social networks predict patch discovery in a wild population of songbirds, *Proceedings of the Royal Society B: Biological Sciences*, 279: 4199-4205.

Araujo, M. S., Guimaraes, P. R., Svanback, R., Pinheiro, A., Guimaraes, P., Dos Reis, S. F. & Bolnick, D. I. (2008), Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets, *Ecology,* 89**:** 1981–1993.

Atton, N. (2010), *Social Learning in Fish*, MPhil Thesis, University of St Andrews.

Atton, N., Hoppitt, W., Webster, M. M., Galef, B. G. and Laland, K. N. (2012), Information flow through threespined stickleback networks without social transmission, *Proceedings of the Royal Society B,* 279: 4272-4278.

Baird, T. A., Ryer, C. H. and Olla, B. L. (1991), Social enhancement of foraging on an ephemeral food source injuvenile walleye Pollock, *Theragra chalcogramma, Environmental Biology of Fishes*, 31: 307–311.

Ballerini, M., Cabibbo, N., Candelier, R, Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M., and Zdravkovic, V. (2008), An empirical study of large, naturally occurring starling flocks: a benchmark in collective animal behaviour, *Animal Behaviour*, 76: 201–215.

Barabasi, A. L. and Oltvai, Z. N. (2004), Network biology: understanding the cell's functional organization, *Nature Reviews Genetics,* 5:101–113.

Barber, I. (2003), Parasites and size-assortative schooling in three-spined sticklebacks, *Oikos,* 101: 331–337.

Barber, I. and Nettleship, S. (2010), From trash fish to supermodel: the rise and rise of the threespined stickleback in evolution and ecology, *Biologist,* 57: 15-21.

Basset, C.E. (1994), Use and evaluation of fish habitat structures in lakes of the eastern United States by the USDA Forest Service, *Bulletin of Marine Science*, 55: 1137–1148.

Beck, M., and Galef, B. G. Jr. (1989), Social influences on the selection of a protein-sufficient diet by Norway rats (*Rattus norvegicus*), *Journal of Comparative Psychology,* 103: 132–139.

Bell, M. A. (1994), Palaeobiology and evolution of the threespined stickleback. *In*, Bell, M. A. and Foster, S. A. *eds.*, *The Evolutionary Biology of the Threespined Stickleback*, p. 438–471. Oxford University Press, Oxford.

Biesmeijer, J. and Seeley, T. (2005), The use of waggle dance information by honey bees throughout their foraging careers, *Behavioural Ecology and Sociobiology*, 59: 133–142.

Boogert, N. J., Reader, S. M., Hoppitt, W. and Laland, K. N. (2008), The origin and spread of innovations in starlings, *Animal Behaviour*, 75: 1509–1518.

Box, H. O. and Gibson, K. R. (eds) (1999), *Mammalian social learning. Comparative and ecological perspectives*, Cambridge, UK: Cambridge University Press.

Boyd, R., and Richerson P. J. (1985), *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R., and Richerson P. J. (1988), An evolutionary model of social learning: The effects of spatial and temporal variation. In *Social Learning: Psychological and Biological Perspectives*, edited by Zentall, T. R. and Galef, B. G. Jr., 29–48. Hillsdale, NJ: Lawrence Erlbaum Assoc.

Bradner, J. and McRobert, S. P. (2001), The effect of shoal size on patterns of body colour segregation in mollies, *Journal of Fish Biology,* 59: 960-967.

Briggs, S. E. Godin, J-G. J., and Dugatkin, L. A., Mate-choice copying under predation risk in the Trinidadian guppy (*Poecilia reticulata*), *Behavioural Ecology*, 7: 151-157.

Briones-Fourzan, P., Ramirez-Zaldivar, E., and Lozano-Alvarez, E. (2008) Influence of conspecific and heterospecific aggregation cues and alarm odours on shelter choice by syntopic spiny lobsters, *The Biological Bulletin,* 215: 182-190.

Brown, G. E. and Godin, J-G. J. (1997), Anti-predator responses to conspecific and heterospecific skin extracts by threespined sticklebacks: alarm pheromones revisited, *Ibis,* 134: 1123–1134.

Brown, C. & Laland, K. N. (2001), Suboski and Templeton revisited: social learning and life skills training for hatchery reared fish, *Journal of Fish Biology*, 59: 471–493.

Brown, C. and Laland, K. N. (2002), Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon, *Journal of Fish Biology,* 61: 987-998.

Brown, C. and Laland, K. N. (2003), Social learning in fishes: a review, *Fish and Fisheries* (Special Edn) 4: 280–288.

Brown, C. and Laland, K. N. (2006), Social learning in fishes. In Fish cognition and behaviour (eds C. Brown, K. N. Laland & J. Krause), pp. 186–202. Oxford, UK: Blackwell Publishing.

Bryant, B. P. and Atema, J. (1987), Diet manipulation affects social behaviour of catfish, *Journal of Chemical Ecology,* 13: 1645-1661.

Bshary, R. And Grutter, A. S. (2006), Image scoring and cooperation in a cleaner fish mutualism, *Nature,* 441: 975-978.

Buckley, N. J. (1996), Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures, *The Auk,* 113: 473-488.

Bumann, D. & Krause, J. (1993), Front individuals lead in shoals of 3-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*), *Behaviour* 125**:** 189–198.

Burnham, K. P. and Anderson, D. R. (2002), *Model selection and multimodel inference: a practical information-theoretic approach,* 2nd edn. New York, NY: Springer.

Byrne, R. W. (1994), The evolution of intelligence. In Slater, P. J. B. and Halliday, T. R. (Eds.), *Behaviour and Evolution*, Cambridge University Press, Cambridge, UK. pp. 223–265.

Candolin, U. (1999), Male–male competition facilitates female choice in sticklebacks, *Proceedings of the Royal Society B,* 266: 785–789.

Childress, M. J. and Herrnkind, W F. (1997), Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence?, *Marine and Freshwater Research*, 48: 751–758.

Childress, M. J., and Herrnkind, W. F. (2001), The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters, *Animal Behaviour,* 62: 465–472.

Chivers, D. P., Brown, G. E., Smith, R. J. F. (1995), Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*) - implications for antipredator behaviour, *Canadian Journal of Zoology*, 73:955–960.

Chivers, D. P. and Smith, R. J. F. (1995), Chemical recognition of risky habitats is culturally transmitted among fathead minnows, *Pimephales promelas* (Osteichthyes, Cyprinidae), *Ethology*, 99: 286-296.

Chou, L. S. and Richerson, P. J. (1992), Multiple models in social transmission of food selection by Norway rats (*Rattus norvegicus*), *Animal Behaviour,* 44: 337–343.

Christley, R. M., Pinchbeck, G. L., Bowers, R. G., Clancy, D., French, N. P., Bennett, R. and Turner, J. (2005), Infection in social networks: Using network analysis to identify high-risk individuals, *American Journal of Epidemiology,* 162: 1024 − 1031.

Coolen, I., van Bergen, Y., Day, R. L. and Laland, K. N. (2003), Species difference in adaptive use of public information in sticklebacks, *Proceedings of the Royal Society of London Series B,* 270: 2413–2419.

Coolen, I., Ward, A. J. W., Hart, P. J. B. and Laland, K. N. (2005), Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues, *Behavioural Ecology,* 16: 865-870.

Corner, L. A. L., Pfeiffer, D. U., and Morris, R. S. (2003), Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*), *Preventive Veterinary Medicine*, 59:147–167.

Coussi-Korbel, S. and Fragaszy, D. M. (1995), On the relation between social dynamics and social learning, *Animal Behaviour*, 50: 1441–1453.

Courtenay, S. C., Quinn, T. P., Dupuis, H. M. C., Groot, C., and Larkin, P. A. (1997), Factors affecting the recognition of population-specific odours by juvenile coho salmon, *Journal of Fish Biology*, 50: 1042-1060.

Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D. and Krause, J. (2003), Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*, *Oikos*, 100: 429-438.

Croft, D. P., James, R., and Krause, J. (2008), *Exploring animal social networks*, Princeton University Press, Princeton.

Croft, D. P., James, R., Thomas, P., Hathaway, C., Mawdsley, D., Laland, K. N. and Krause, J. (2006), Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata), Behavioural Ecology and Sociobiology*, 59: 644–650.

Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D. and Krause, J. (2005), Assortative interactions and social networks in fish, *Oecologia*, 143: 211–219.

Croft, D. P., Krause, J. and James, R. (2004), Social networks in the guppy (*Poecilia reticulata), Proceedings of the Royal Society of London B,* 271: 516–519.

Cross, P. C., Lloyd-Smith, J. O., Bowers, J. A., Hay, C. T., Hofmeyr, M., and Getz, W. M. (2004), Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park, *Annales Zoologici Fennici,* 41:879–892.

Danchin, E., Boulinier, T. & Massot, M. (1998), Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality, *Ecology*, 79: 2415–2428.

Danchin É., Giraldeau, L. A., Valone, T. J. and Wagner, R. H. (2004), Public information: from nosy neighbors to cultural evolution, *Science*, 305: 487-491.

Darby, C. L. and Riopelle, A. J. (1959), Observational learning in the rhesus monkey, *Journal of Comparative and Physiological Psychology*, 52:94–98.

Day, R., MacDonald, T., Brown, C., Laland, K. N., and Reader, S. M. (2001), Interactions between shoal size and conformity in guppy social foraging, *Animal Behaviour,* 62: 917–925.

Dekker, D., Krachhardt, D. &Snijders, T. (2007), Sensitivity of MRQAP tests to collinearity and autocorrelation conditions, *Psychometrika*, 72: 563-581.

Deutsch, J. C. and Nefdt, R. J. C. (1992), Olfactory cues influence female choice in two lek-breeding antelopes, *Nature,* 356: 596.

Doligez, B., Danchin, E., and Clobert, J. (2002), Public information and breeding habitat selection in a wild bird population, *Science,* 297:1168–1170.

Donahue, M.J. (2006), Allee effects and conspecific cueing jointly lead to conspecific attraction, *Oecologia*, 149: 33–43.

Dugatkin, L. A. (1992), Sexual selection and imitation: females copy the mate choice of others, *American Naturalist,* 139: 1384-1489.

Dugatkin, L. A., Fitzgerald, G. J. and Lavoie, J. (1994), Juvenile three-spined sticklebacks avoid parasitized conspecifics, *Environmental Biology of Fishes,* 39: 215-218.

Dugatkin, L. A. and Godin J-G. J. (1992), Reversal of mate choice by copying in the guppy (*Poecilia reticulata*), *Proceedings of the Royal Society of London Series B*, 249: 179-184.

Dugatkin, L. A. and Godin J-G. J. (1993), Female mate choice copying in the guppy (*Poecilia reticulata*): age dependent effects, *Behavioural Ecology,* 4: 289-292.

Dunbar, R. I. M. (1992), Time: a hidden constraint on the behavioural ecology of baboons, *Behavioural Ecology and Sociobiology*, 31:35–49.

Dunne, J. A., Williams, R. J. and Martinez, N. D. (2002), Food-web structure and network theory: the role of connectance and size, *Proceedings of the National Academy of Science USA*, 99:12917–12922.

Early, R. L. and Dugatkin, L. A. (2002), Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking, *Proceedings of the Royal Society of London B*, 269: 943–952.

Eggleston, D. B. and Lipcius, R. N. (1992), Dynamics of shelter selection by Caribbean spiny lobster under variable predation risk, social conditions and shelter size, *Ecology,* 73: 992-1011.

Ellis, T., James, J. D., Stewart, C. and Scott, A. P. (2004), A non-invasive stress assay based upon measurement of free cortisol released into the water by rainbow trout, *Journal of Fish Biology,* 65: 1233-1252.

Feldman, M. W.,Aoki, K. and Kumm, J. (1996), Individual versus social learning: Evolutionary analyses in a fluctuating environment, *Anthropologiocal Science,* 104: 209–231.

Fischhoff, I. R., Dushoff, J. Sundaresan, S. R., Cordingley, J. E. and Rubenstein, D. I. (2009), Reproductive status influences group size and persistence of bonds in male plains zebra (*Equus burchelli*), *Behavioural Ecology and Sociobiology,* 63: 1035-1043.

Fisher, J. and Hinde, R. A. (1949), The opening of milk bottles by birds, *British Birds,* 42: 347–357.

FitzGerald, G. J. and Wootton, R. J. (1996), The behavioural ecology of sticklebacks. In *Behaviour of teleost fishes*, 2nd edn (ed. T. J. Pitcher), pp. 537–572. Fish and fisheries series 7. London: Chapman & Hall.

Flack, J.C., Girvan, M., de Waal, F. B. M., Krakauer, D. C. (2006), Policing stabilizes construction of social niches in primates, *Nature*, 439:426–429

Forsman, J., and Seppanen, J. (2011), Learning what (not) to do: Testing rejection and copying of simulated hetrospecific behavioural traits, *Animal Behaviour,* 81: 879–883.

Foster, S. A. (1988), Diversionary displays of paternal stickleback. Defences against cannibalistic groups, *Behavioural Ecology and Sociobiology,* 22: 335-340.

Foster, S. A. (1994), Evolution of reproductive behavior of threespined stickleback. In: Bell, M. A. and Foster, S. A. (eds.), *The Evolutionary Biology of the Threespined Stickleback*. Oxford: Oxford University Press, 381–398.

Franz, M. and Nunn, C. L. (2009), Network-based diffusion analysis: a new method for detecting social learning, *Proceedings of the Royal Society B*, 276: 1829–1836.

Freeman, S. (1987), Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests, *Behavioural Ecology and Sociobiology*, 21: 307–311.

Fretwell, S. D. and Lucas, H. L. (1970), On territorial behavior and other factors influencing habitat distribution in birds, 1. Theoretical development, *Acta Biotheoretica*, 19: 16-36.

Frommen, J. G. & Bakker, T. C. M. (2004), Adult three-spined sticklebacks prefer to shoal with familiar kin, *Behaviour,* 141: 1401–1409.

Frommen, J. G., Luz, C. and Bakker, T. C. M. (2007a), Nutritional state influences shoaling preference for familiars, *Zoology,* 110**:** 369–376.

Frommen, J. G., Luz, C., and Bakker, T. (2007b), Kin discrimination in sticklebacks is mediated by social learning rather than innate recognition, *Ethology*, 113: 276-282.

Fryday, S. L. and Grieg-Smith, P. W. (1994), The effects of social learning on the food choice of the house sparrow (*Passer domesticus*), *Behaviour*, 128: 281–300.

Galef, B. G. Jr. (1986), Social interaction modifies learned aversions, sodium appetite, and both palatability and handling-time induced dietary preference in rats (*Rattus norvegicus*), In Zentall, T. R. and Galef, B. G. Jr, (Eds.), *Social Learning: Psychological and biological perspectives,* Hillsdale, NJ, Erlbaum, pp. 119-139.

Galef, B. G. Jr. (1988), Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In *Social Learning: Psychological and Biological Perspectives* (ed. T. *R.* Zentall and B. G. Galef), pp. 3-28. Erlbaum, Hillsdale, NJ.

Galef, B. G. Jr. (1992), The question of animal culture, *Human Nature*, 3: 157–178.

Galef, B. G. Jr. (1993), Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission, *Animal Behaviour,* 46: 257-265.

Galef, B. G., Jr. (2005), *Social learning*. In: The Behavior of the Laboratory Rat: a Handbook with Tests (Ed. by I. Q. Whishaw & B. Kolb), pp. 363-370. Oxford: Oxford University Press.

Galef, B. G. Jr and Beck, M. (1985), Aversive and attractive marking of toxic and safe foods by Norway rats, *Behavioural and Neural Biology,* 43: 298-310.

Galef, B. G. Jr., Dudley, K. E., and Whiskin, E. E. (2008), Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats, *Animal Behaviour,* 75: 631–637.

Galef, B. G. Jr., Marczinzki, C. A., Murray, K. A. and Whiskin, E. E. (2001), Food stealing by young Norway rats (*Rattus norvegicus*), *Journal of Comparative Pyschology*, 115: 16-21.

Galef, B. G. Jr, McQuoid, L. and Whiskin, E. E. (1990), Further evidence that Norway rats do not transmit socially learned aversions to toxic baits, *Animal Learning and Behaviour,* 18: 199-205.

Galef, B. G. Jr. and Wigmore, S. W. (1983), Transfer of information concerning distant foods: A laboratory investigation of the "information centre" hypothesis, *Animal Behaviour,* 31: 748-758.

Galef, B. G. Jr., Wigmore, S. W., and Kennett, D. J. (1983), A failure to find socially mediated taste aversion learning in Norways rats (*R. norvegicus*), *Journal of Comparative Psychology,* 97: 358-363.

Gibson G. (2005), The synthesis and evolution of a supermodel, *Science,* 307: 1890-1891.

Gibson, R. M. and Hoglund, J. (1992), Copying and Sexual Selection, *Trends in Ecology and Evolution*, 7: 229-232.

Gill, A. B. and Hart, P. J. B. (1998), Stomach capacity as a directing factor in prey size selection of three-spined stickleback, *Journal of Fish Biology,* 53**:** 897–900.

Giraldeau, L. A., Valone, T. J. and Templeton J. J. (2002), Potential disadvantages of using socially acquired information, *Philisophical Transactions of the Royal Society of London B,* 357: 1559–1566.

Godfrey, S., Bull, M., James, R., and Murray, K. (2009), Network structure and parasite transmission in a group living lizard, the gidgee skink (*Egernia stokes), Behavioural Ecology and Sociobiology,* 63: 1045-1056.

Godin, J-G. J. and Hair, K. P. E. (2009), Mate-choice copying in free-ranging Trinidadian guppies (*Poecilia reticulata*), *Behaviour,* 146: 1443-1461.

Goldschmidt, T., Bakker, T. C. M. and Feuth-de Bruijn, E. (1993), Selective copying in mate choice of female sticklebacks, *Animal Behaviour,* 45: 541-547.

Gotceitas, V. And Colgan, P. (1991), Assessment of patch profitability and ideal free distribution: The significance of sampling, *Behaviour,* 119: 1-2.

Grant, J. W. and Green L. D. (1996), Mate copying versus preferences for actively courting males by Japanese medaka (*Oryzias latipes*), *Behavioural Ecology,* 7: 165-167.

Griffiths, S. W. And Magurran, A. E. (1997a), Schooling preferences for familiar fish vary with group size in a wild guppy population, *Proceedings of the Royal Society B,* 264: 547-551.

Griffiths, S. W. And Magurran, A. E. (1997b), Familiarity in schooling fish: how long does it take to acquire?, *Animal Behaviour,* 53: 945-949.

Griffiths, S. W. and Ward, A. J. W. (2006), Learned recognition of conspecifics. In Brown, C., Laland, K. N. and Krause, J., *Fish Cognition and Behaviour*, Blackwell, Oxford, pp. 139-157.

Grosenick, L., Clement, T. S. and Fernald, R. D. (2007), Fish can infer social rank by observation alone, *Nature*, 445: 429–432.

Gruter, C., Sol Balbuena, M. and Farina, W. M. (2008), Informational conflicts created by the waggle dance, *Proceedings of the Royal Society B,* 275: 1321–1327.

Grutter, A. S. and Bshary, R. (2003), Cleaner wrasse prefer client mucus: support for partner control mechanisms in cleaning interactions, *Proceedings of the Royal Society B,* 270: S242-S244.

Hall, D. and Suboski, M. D. (1995), Visual and olfactory stimuli in learned release of alarm reactions by zebra danio fish (*Brachydanio rerio*), *Neurobiology of Learning and Memory*, 63: 229–240.

Hart, P. J. B. and Gill, A. B. (1994), Evolution of foraging behaviour in threespined stickleback. In: Bell, M. A. and Foster, S. A. (eds.), *The Evolutionary Biology of the Threespined Stickleback,* Oxford: Oxford University Press, 207–239.

Helfman, G. S. and Schultz, E. T. (1984), Social transmission of behavioural traditions in a coral reef fish, *Animal Behaviour*, 32: 379–384.

Henzi, S. P., Lusseau, D., Weingrill, T., van Schaik, C. P., and Barrett, L. (2009), Cyclicity in the structure of female baboon social networks, *Behavioural Ecology and Sociobiology*, 63: 1015-1021.

Hess, K. & Gentleman, R. (2010), muhaz: Hazard Function Estimation in Survival Analysis. R package version 1.2.5.http://CRAN.R-project.org/package=muhaz(S original by Kenneth Hess and R port by R. Gentleman).

Heyes, C. M. (1994), Social learning in animals: Categories and mechanisms, *Biological Reviews*, 69: 207-231.

Heyes, C. M. and Galef Jr, B. G. (eds) (1996), Social *learning in animals. The roots of culture*, San Diego, CA: Academic Press Inc.

Hinde, R. A. (1976), Interactions, relationships and social-structure, *Man,* 11:1–17.

Hinde, R. A. and Fisher, J. (1951), Further observations on the opening of milk bottles by birds, *British Birds*, 44: 393–396.

Hixon, M. A. and Beets, J. P. (1989), Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs, *Bulletin of Marine Science,* 44: 666-680.

Hoare, D. J., Ruxton, G. D., Godin, J. G. J. and Krause, J. (2000), The social organisation of free-ranging fish shoals, *Oikos*, 89: 546-554.

Höjesjö, J., Johnsson, J. I., Petersson, E., and Jarvi, T. (1998), The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*), *Behavioural Ecology*, 9:445–451.

Holbrook, S.J. and Schmitt, R.J. (1984), Experimental analyses of patch selection by foraging black surfperch (*Embiotoca jacksoni* Agazzi), *Journal of Experimental Marine Biology and Ecology*, 79: 39–64.

Holbrook, S. J. and Schmitt, R. J. (2002), Competition for shelter space causes density-dependent predation mortality in damselfishes, *Ecology,* 83: 2855–2868.

Hoogland, R. D., Mooris, D. and Tinbergen, N. (1957), The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defence against predators (*Perca* and *Esox*), *Behaviour,* 10: 205–237.

Hopewell, L. J., Leaver, L. A., Lea, S. E. G. And Wills, A. J. (2010), Grey squirrels (*Sciurus carolinensis*) show a feature-negative effect specific to social learning, *Animal Cognition,* 13: 219-227.

Hoppitt, W., Blackburn, L., and Laland, K. N. (2007), Response facilitation in the domestic fowl, *Animal Behaviour,* 73: 229–238.

Hoppitt, W. J. E., Boogert, N. J. and Laland, K. N. (2010a), Detecting social transmission in networks, *Journal of Theoretical Biology,* 263: 544–555.

Hoppitt, W., Kandler, A., Kendal, J. R. and Laland, K. N. (2010b), The effect of task structure on diffusion dynamics: implications for diffusion curve and network-based analysis, *Learning & Behaviour*, 38: 243–251.

Hoppitt, W. and Laland, K. N. (2008), Social processes influencing learning in animals: A review of the evidence, *Advances in the study of animal behaviour,* 38: 105-165.

Hoppitt, W. J. and Laland, K. N. (2011), Detection of social learning using networks: a user's guide, *American Journal of Primatology,* 72: 834–844.

Hoppitt, W. and Laland, K. N. (2013), *Social Learning. An introduction to mechanisms, methods and models,* Princeton University Press, Princeton and Oxford.

Horner, A. J., Nickles, S. P., Weissburg, M. J. and Derby, C. D. (2006), Source and specificity of chemical cues mediating shelter preference of Caribbean spiny lobsters (*Panulirus argus*), *The Biological Bulletin*, 211: 128-139.

Houde, A. (1997), *Sex, colour and mate choice in guppies,* Princeton University Press, Princeton.

Houseal, G. A. and Olson, B. E. (1995), Cattle use of microclimates on a northern latitude winter range, *Canadian Journal of Animal Science,* 75: 501-507.

Huntingford, F. A. and Ruiz-Gomez, M. L. (2009), Three-spined sticklebacks *Gasterosteus aculeatus* as a model for exploring behavioural biology, *Journal of Fish Biology,* 75: 1943-1976.

Ioannou, C. C., Payne, M. and Krause, J. (2008), Ecological consequences of the bold-shy continuum: the effect of predator boldness on prey risk, *Oecologia,* 157: 177–182.

Jamieson, I. G. (1995), Do female fish prefer to spawn in nests with eggs for reasons of mate choice copying or egg survival?, *American Naturalist*, 145:824–832.

Jara, F. and Cespedes, R. (1994), An experimental evaluation of habitat enhancement on homogeneous marine bottoms in southern Chile, *Bulletin of Marine Science*, 55: 295–307.

Johnston, D. H. (1999), The insignificance of statistical significance testing, *Journal of Wildlife Management*, 63: 763–772.

Johnston, A. N. B., Burne, T. H. J. and Rose, S. P. R. (1998), Observation learning in day-old chicks using a one-trial passive avoidance learning paradigm, *Animal Behaviour*, 56: 1347–1353.

Kaiser, D. H., Zentall, T. R., and Galef, B. G., Jr. (1997), Can imitation in pigeons be explained by local enhancement together with trial and error learning?, *Psychological Science*, 8: 459–460.

Kawahara, R., Miya, M., Mabuchi, K., Near, T. J., and Nishida, M. (2009), Stickleback phylogenies resolved: Evidence from mitochondrial genomes and 11 nuclear genes, *Molecular Phylogenetics and Evolution,* 50: 401-404.

Kawai, M. (1965), Newly-acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima Islet, *Primates*, 6: 1–30.

Kendal, R. L., Coolen, I. van Bergen, Y. and Laland, K. N. (2005), Tradeoffs in the adaptive use of social and asocial learning, *Advances in the Study of Behaviour*, 35: 333–379.

Kendal, R. L., Custance, D. M., Kendal, J. R., Vales, G., Stoinski, T. S., Rakotomalala, N. L. and Rasamimanana H. (2010), Evidence for social learning in wild lemurs (*Lemur catta*), *Learning and Behaviour,* 38: 220–234.

Kendal, J. R., Rendell, L., Pike, T. W. and Laland, K. N. (2009), Nine-spined sticklebacks deploy a hill-climbing social learning strategy, *Behavioural Ecology,* 20: 238-244.

Kingsley, D. M. and Peichel, C. L. (2007), The molecular genetics of evolutionary change in sticklebacks. In *Biology of the Three-Spined Stickleback* (ed. Östlund-Nilsson, S., Mayer, I. and Huntingford, F.), pp. 41-81. Boca Raton: CRC Press.

Kohler, D. (1976), The interaction between conditioned fish and naive schools of juvenile carp (*Cyprinus carpio*, Pisces), *Behavioural Processes*, 1: 267–275.

Kraak, S. B. M., Bakker, T. C. M. & Mundwiler, B. (1999), Sexual selection in sticklebacks in the field: correlates of reproductive, mating, and paternal success, *Behavioral Ecology,* 10: 696–706.

Krause, J. (1993a), The effect of "Schreckstoff" on the shoaling behaviour of the minnow: A test of Hamilton's selfish herd theory, *Animal Behaviour*, 45: 1019-1024.

Krause, J. (1993b), Positioning behaviour in fish shoals: a cost-benefit analysis, *Journal of Fish Biology*, 43: 309–314.

Krause, J., Hoare, D. J., Croft, D., Lawrence, J., Ward, A., Ruxton, G. D., and James, R. (2000a), Fish shoal composition: mechanisms and constraints, *Proceedings of the Royal Society of London Series B*: *Biological Sciences*, 267: 2011-2017.

Krause, J., Butlin, R. K., Peuhkuri, N., and Pritchard, V. L. (2000b), The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field, *Biological Reviews*, 75: 477-501.

Krause, J., and Ruxton, G. D. (2002), *Living in groups*, Oxford University Press.

Krause, J., Croft, D. P. and James, P. (2007), Social network theory in the behavioural sciences: potential applications, *Behavioural Ecology and Sociobiology,* 62: 15-27.

Krause, J. and Godin, J-G. J. (1996), Influence of parasitism on shoal choice in the banded killifish (*Fundulus diaphanus,*Teleosti*,*Cyprinodontidae), *Ethology,* 102: 40-49.

Krause, J., Godin, J-G. J. and Brown, D. (1996), Size-assortiveness in multi-species fish shoals, *Journal of Fish Biology,* 49: 221-225.

Krause, J. & Tegeder, R. W. (1994), The mechanism of aggregation behavior in fish shoals –individuals minimize approach time to neighbours, *Animal Behaviour,* 48: 353–359.

Krebs, J. R., MacRoberts, M. H., and Cullen, J. M. (1972), Flocking and feeding in the great tit *Parus major*: an experimental study, *Ibis*, 114: 507–530.

Lachlan, R., Crooks, L., and Laland, K. N. (1998), Who follows whom? Shoaling preferences and social learning of foraging information in guppies, *Animal Behaviour,* 56: 181–190.

Laegdsgaard, P. and Johnson, C. (2001), Why do juvenile fish utilise mangrove habitats?, *Journal of Experimental Marine Biology and Ecology*, 257: 229–253.

Laland, K. N. (2004), Social learning strategies. *Learning and Behaviour,* 32: 4–14.

Laland, K. N.and Galef, B. G. Jr. (2009), *The question of animal culture,* Harvard University Press, U.S.A.

Laland, K. N. and Reader, S. (1999), Foraging innovation in the guppy, *Animal Behaviour,* 57: 331-340.

Laland, K. N. and Williams, K. (1997), Shoaling generates social learning of foraging information in guppies, *Animal Behaviour,* 53: 1161-1169.

Laland, K. N. and Williams, K. (1998), Social transmission of maladaptive information in the guppy, *Behavioural Ecology,* 9*:* 493-499.

Laland, K. N., Atton, N., and Webster, M. M. (2011), From fish to fashion: experimental and theoretical insights into the evolution of culture, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366: 958-968.

Laughlin, S. B. and Sejnowski, T. J. (2003), Communication in neuronal networks, *Science*, 301:1870–1874.

Leadbeater, E. and Chittka, L. (2007), The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*), *Behavioural Ecology and Sociobiology,* 61: 1789–1796.

Lefebvre, L. (1995a), Culturally-transmitted feeding behaviour in primates: evidence for accelerated learning rates, *Primates,* 36: 227-239.

Lefebvre, L. (1995b), The opening of milk bottles by birds: Evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission, *Behavioural Processes,* 34: 43-53.

Lefebvre, L., and Palameta, B. (1988), Mechanisms, ecology and population diffusion of socially learned, food-finding behaviour in feral pigeons. In *Social Learning: Psychological and Biological Perspectives*, edited by B. G. Galef, Jr. and Zentall, T. R., 141–164. Hillsdale, NJ: Erlbaum

Lefebvre, L., and Giraldeau, L. (1994), Cultural transmission in pigeons is affected by the number of tutors and bystanders present, *Animal Behaviour,* 47: 331–337.

Lupfer, G., Frieman, J., and Coonfield, D. (2003), Social Transmission of Flavor Preferences in Two Species of Hamsters (*Mesocricetus auratus* and *Phodopus campbelli*), *Journal of Comparative Pyschology,* 117: 449-455.

Lupfer-Johnson, G. and Ross, J. (2007), Dogs acquire food preferences from interacting with recently fed conspecifics, *Behavioural Processes,* 74: 104-106.

Lusseau, D. (2002), The emergent properties of a dolphin social network*, Proceedings of the Royal Society of London B*, 270: 186–188.

Lusseau, D., and Newman, M. E. J. (2004), Identifying the role that animals play in their social networks, *Proceedings of the Royal Society of London B* (Suppl), 271:S477–S481.

Mackney, P. A. & Hughes, R. N. (1995), Foraging behaviour and memory window in sticklebacks, *Behaviour* 132**:** 1241–1253.

Magurran, A. E. & Higham, A. (1988), Information transfer across fish shoals under predator threat, *Ethology*, 78: 153–158.

Manicom, C., Schwarzkopf, L., Alford, R. A. and Schoener, T. W. (2008), Self-made shelters protect spiders from predation, *Proceedings of the National Academy of Sciences U.S.A.*, 105: 14903-14907.

Manly, B. (2008), *Randomization, Bootstrap and Monte Carlo Methods in Biology, 3rd Ed*. London: Chapman and Hall.

Marconato, A. and Bisazza, M. (1986), Males whose nests contain eggs are preferred by female *Cottus gobio, Animal Behaviour,* 34: 1580-1582.

Mason, J. R. and Reidinger, R. F. (1982), Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*), *Auk*, 99: 548–554.

Mason, J. R. and Reidinger, R. F. (1983), Importance of color for methiocarb-induced food aversions in red-winged blackbird, *Journal of Wildlife Management*, 47: 383–393.

Mateo, J. M. (2004), Recognition systems and biological organisation: The perception component of social recognition, *Annales Zoologici Fennici,* 41: 729 – 745.

Matsumura, K., Matsunaga, S. and Fusetani, N. (2004), Possible involvement of phospatidylcholine in school recognition in the catfish (*Plotosus lineatus), Zoological Science,* 21: 257-264.

Matsumura, K., Matsunaga, S., and Fusetani, N. (2007), Phosphatidylcholine profile-mediated group recognition in catfish, *The Journal of Experimental Biology,* 210: 1992-1999.

McGregor, P. K. (1993), Signalling in territorial systems - a context for individual identification, ranging and eavesdropping, *Philosophical Transactions of the Royal Society of London B*, 340: 237–244.

McKinnon, J. S. and Rundle, H. D. (2002), Speciation in nature: the threespined stickleback model systems, *Trends in Ecology and Evolution,* 17: 480-488.

McPhail, J. D. (1984), Ecology and evolution of sympatric sticklebacks (Gasterosteus): Morphological and genetic evidence for a species pair in Enos Lake, British Columbia, *Canadian Journal of Zoology,* 62: 1402-1408.

Menzel, E. W. Jr., (1974), A group of young chimpanzees in a one acre field. In *Behavior of Nonhuman Primates: Modern Research Trends*, edited by Schrier, A. M. and Stollnitz, F., 83–153. Vol. 5, *Precultural Primate Behavior*, New York: Academic Press.

Milinski, M. and Heller, R. (1978), Influence of a predator on optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus* L), *Nature,* 275: 642–644.

Milinski, M. and Bakker, T. C. M. (1990), Female sticklebacks use male coloration in mate choice and hence avoid parasitized males, *Nature,* 344: 330–333.

Milinski, M., Kulling, D. and Kettler, R. (1990), Tit-for-Tat in sticklebacks *Gasterosteus aculeatus*: trusting a cooperating partner, *Behavioral Ecology,* 1: 7–11.

Mineka, S. and Cook, M. (1988), Social learning and the acquisition of snake fear in monkeys. In *Social Learning: Psychological and Biological Perspectives* (ed. T. R. Zentall and B. G. Galef), pp. 51-74. Erlbaum, Hillsdale, NJ.

Morgan, B. J. T. (2009), Applied Stochastic Modelling. 2nd edition. Boca Raton: Chapman & Hall/ CRC Press.

Moore, B. R. (1992), Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning, *Behaviour,* 122: 231–263.

Moore, A., Ives, M. J., and Kell, L. T. (1994), The role of urine in sibling recognition in Atlantic salmon *Salmosalar (L.) parr*, *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 255: 173-180.

Morrell, L. J., Hunt, K. L., Croft, D. P. and Krause, J. (2007), Diet, familiarity and shoaling decisions in guppies, *Animal Behaviour,* 74: 311-319.

Munger, S. D., Leinders-Zufall, T., McDougall, L. M., Cockerham, R. E., Schmid, A., Wandernoth, P., Wennemuth, G., Biel, M., Zufall, F. and Kelliher, K. R. (2010), An olfactory subsystem that detects carbon disulfide and mediates food-related social learning, *Current Biology,* 20: 1438-1444.

Newman, M. E. J. (2003), The structure and function of complex networks, *SIAM Review*, 45:167–256.

Newman, M. E. J. (2009), *Networks: An introduction,* Oxford University Press, Oxford.

Oliveira, R. F., McGregor, P. K. and Latruffe, C. (1998), Know thine enemy: fighting fish gather information from observing conspecific interactions, *Proceedings of the Royal Society of London B*, 265: 1045–1049.

Olsen, K. H., Grahn, M., and Lohm, J. (2003), The influence of dominance and diet on individual odours in MHC identical juvenile Arctic charr siblings, *Journal of Fish Biology,* 63: 855–862.

Pardo, L.M. and Johnson, L. E. (2006), Influence of water motion and reproductive attributes on movement and shelter use in the marine snail *Littorina saxatilis, Marine Ecology Progress Series,* 315: 177-186.

Patriquin-Meldrum, K. J. and Godin, J-G. J. (1998), Do Female Three-Spined sticklebacks Copy the Mate Choice of Others?, *The American Naturalist,* 151: 570-577.

Pearce, J. M. (1997), *Animal Learning and Cognition. An Introduction. 2nd edition,* Pyschology Press, Hove, UK.

Peichel, C. L., Nereng, K. S., Ohgi, K. A., Cole, B. L. E., Colosimo, P. F., Buerkle, C. A., Schulter, D. and Kingsley, D. M. (2001), The genetic architecture of divergence between threespined stickleback species, *Nature,* 414: 901-905.

Pike, T. W., Samanta, M., Lindstrom, J. & Royle, N. J. (2008), Behavioural phenotype affects social interactions in an animal network, *Proceedings of the Royal Society B* 275: 2515–2520.

Pitcher, T. J., Magurran, A. E and Edwards, J. I. (1985), Schooling mackerel and herring choose neighbours of similar size, *Marine Biology,* 86: 411-416.

Pitcher, T. J., Magurran, A. E and Allan, J. R. (1986), Size segregative behaviour in minnow shoals, *Journal of Fish Biology,* 29: 83-95.

Pitcher, T. J. and Parrish, J. K. (1993) Functions of shoaling behaviour in teleosts. In *The behaviour of teleost fishes* (ed. T. J. Pitcher), pp. 363–439, 2nd edn. London, UK: Croom Helm.

Potterat, J. J., Muth, S. Q., Rothenberg, R. B., Zimmerman-Rogers, H., Green, D. L., Taylor, J. E., Bonney, M. S. and White, H. A. (2002), Sexual network structure as an indicator of epidemic phase, *Sexually Transmitted Infections*, 78:152–15.

R Development Core Team (2010), R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ramos-Fernandez, G., Boyer, D., and Gomez, V. P. (2006), A complex social structure with fission–fusion properties can emerge from a simple foraging model, *Behavioural Ecology and Sociobiology*, 60: 536–549.

Ratcliffe, J. M. and ter Hofstede, H. M. (2005), Roosts as information centres: social learning of food preferences in bats, *Biology Letters,* 1: 72-74.

Reader, S. M. (2004), Distinguishing social and asocial learning using diffusion dynamics, *Learning & Behavior*, 32: 90-104.

Reader, S. M. and Laland, K. N. (2000), Diffusion of foraging information in the guppy, *Animal Behaviour*, 60: 175–180.

Reader, S. M. and Laland, K. N. (2003), Animal innovation: an introduction. In *Animal innovation* (eds S. M. Reader & K. N. Laland), pp. 3–35. Oxford, UK: Oxford University Press.

Reebs, S. G. (2000), Can a minority of informed leaders determine the foraging movements of a fish shoal?, *Animal behaviour,* 59: 403 – 409.

Reebs, S. G. (2001), Influence of body size on leadership in shoals of golden shiners, *Notemigonus Crysoleucas, Behaviour,* 138: 797-809.

Reimchen, T. E. (1994), Predators and morphological evolution in threespined stickleback. In: Bell, M. A. and Foster, S. A. (eds.), *The Evolutionary Biology of the Threespined Stickleback.* Oxford: Oxford University Press, 240–276.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T., and Laland, K. N. (2010), Why copy others? Insights from the Social Learning Strategies Tournament, *Science* 328: 208-213.

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M. and Laland, K. N. (2011), Cognitive culture: theoretical and empirical insights into social learning strategies, *Trends in Cognitive Sciences*, 15: 68–76.

Rescorla, A. (1988), Behavioral studies of Pavlovian conditioning, *Annual Review of Neuroscience* XI: 329-352**.**

Reynolds, J.D. and Jones, J. C. (1999), Female preference for preferred males is reversed under low oxygen conditions in the common goby (*Pomatoschistus microps*), *Behavioural Ecology,* 10: 149-154.

Ridley, M. & Rechten, C. (1981), Female sticklebacks prefer to spawn with mates whose nests contain eggs, *Behaviour,* 16: 152-161.

Ruxton, G. D., Speed, M. P. and Kelly, D. J. (2004), What, if anything, is the adaptive function of countershading?, *Animal Behaviour,* 68: 445-451.

Ryan, M. J. (1997), Sexual Selection and Mate Choice in Krebs J. R. & Davies N. B. (Eds), (1997), *Behavioural Ecology. An Evolutionary Approach. Fourth Edition,* Blackwell Science Ltd., Cambridge.

Saleh, N., Ohashi, K., Thomson, J. D. and Chittka, L. (2006), Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers, *Animal Behaviour*, 71: 847–854.

Salvanes, A. G. V. and Hart, P. J. B. (1998), Individual variability in state-dependent feeding behaviour in three-spined sticklebacks, *Animal Behaviour,* 55: 1349–1359.

Sargent, R. C. (1988), Parental care and egg survival both increase with clutch size in the fathead minnow, *Pimephales promelas, Behavioral Ecology and Sociobiology*, 23:33–37.

Sarin, S., and Dukas, R. (2009), Social learning about egg laying substrates in fruit flies, *Proceedings of the Royal Society B,* 276: 4323–4328.

Schlupp, I., Marler, C. and Ryan, M. J. (1994), Benefit to male sailfin mollies of mating with heterospecific females, *Science*, 267: 373-374.

Schlupp, I. and Ryan, M. J. (1997), Male sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males, *Behavioural Ecology*, 8: 104-107.

Schuster, S., Wohl, S., Griebsch, M. and Klostermeier, I. (2006), Animal cognition: how archer fish learn to down rapidly moving targets, *Current Biology*, 16: 378–383.

Schwarzkopf, L. And Alford, R. A. (1996), Dessication and shelter-site use in a tropical amphibian: comparing toads with physical models, *Functional Ecology,* 10: 193-200.

Scott, J. (2000), *Social network analysis,* Sage, London.

Sen, P., Dasgupta, S., Chatterjee, A., Sreeram, P. A., Mukherjee, G. and Manna, S. S. (2003), Small-world properties of the Indian railway network, *Physical Review E,* 67: 036106

Seppa, T., Laurila, A., Peuhkuri, N., Piironen, J., and Lower, N. (2001), Early familiarity has fitness consequences for Arctic char (*Salvelinus alpinus*) juveniles, *Canadian Journal of Fisheries and Aquatic Science*, 58:1380–1385.

Seppanen, J., Forsman, J., Monkkonen, M., Krams, I., and Salmi, T. (2011), New behavioural trail adopted or rejected by observing heterospecific tutor fitness, *Proceedings of the. Royal Society B,* 278:1736–1741.

Sherry, D. F. and Galef, B. G. Jr. (1984), Cultural transmission without imitation: Milk bottle opening by birds, *Animal Behaviour* 32: 937–938.

Sih, A. Hanser, S. F. and McHugh, K. A. (2009), Social network theory: new insights and issues for behavioral ecologists, *Behavioural. Ecology and Sociobiology,* 63:975–988.

Smith, J. W., Benkman, C. W. and Coffey, K. (1999), The use and mis-use of public information by red crossbills, *Behavioural. Ecology*, 10: 54-62.

Spence, K. (1937), Experimental studies of learning and higher mental processes in infra-human primates, *Psychological Bulletin*, 34: 806–850.

Suboski, M. D., Bain, S., Carty, A. E., McQuoid, L. M., Seelen, M. I. and Seifert, M. (1990), Alarm reaction in acquisition and social transmission of simulated-predator recognition by zebra danio fish (*Brachydanio rerio*), *Journal of Comparative Psychology*, 104: 101-112.

Sugita, Y. (1980), Imitative choice behavior in guppies, *Japanese Pyschological Research,* 22: 7–12.

Swaney, W., Kendal, J., Capon, H., Brown, C. and Laland, K. N. (2001), Familiarity facilitates social learning of foraging behaviour in the guppy, *Animal Behaviour*, 62: 591–598.

Tadic, B. (2001), Dynamics of directed graphs: the World-Wide Web, *Physica A,* 293: 273–284.

Templeton, J.J. (1998), Learning from others' mistakes: a paradox revisited, *Animal Behaviour*, 55: 79–85.

Templeton, J. J. and Giraldeau, L.-A. (1995), Patch assessment in foraging flocks of European starlings: evidence for the use of public information, *Behavioural Ecology,* 6: 65-72.

Templeton, J. J. and Giraldeau, L.-A. (1996), Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment, *Behavioural Ecology and Sociobiology,* 38: 105-114.

Thorndike, E. L. (1898), *Animal intelligence: An experimental study of the associative processes in animals*, Macmillan, New York.

Thorpe, W. H. (1956), *Learning and Instinct in Animals.* Methuen, London.

Thorpe, W. H. (1963), *Learning and instinct in animals*, 2nd ed. London.

Therneau, T.M. &Grambsch, P.M. (2000), Modeling survival data: extending the Cox model. New York: Springer.

Treherne, J. E. and Foster, W. A. (1981), Group Transmission of predator avoidance behaviour in a marine insect: The Trafalgar effect, *Animal Behaviour,* 29: 911-917.

Utne-Palm, A. C. and Hart, P. J. B. (2000), The effects of familiarity on competitive interactions between threespined sticklebacks, *Oikos*, 91:225–232.

Valone, T. J. (1989), Group foraging, public information, and patch estimation, *Oikos,* 56: 357–363.

Valone, T. J. (2007), From eavesdropping on performance to copying the behavior of others: a review of public information use, Behavioral *Ecology and Sociobiology*, 62: 1-14.

Valone, T. J. and Templeton, J. J. (2002), Public information for the assessment of quality: a widespread social phenomenon, *Philisophical Transactions of The Royal Society B,* 357: 1549-1557.

Valsecchi, P and Galef, B. G. Jr. (1989), Social influences on the food preferences of house mice (*Mus musculus)*, *The International Journal of Comparative Pyschology,* 2: 245-256.

Visalberghi, E. (1994), Learning process and feeding behaviour in monkeys. In Galef, B. J., Mainardi, M. And Valsecchi, P., *Behavioural Aspects of Feeding: Basic and Applied Research on Mammals,* Harwood Academic Publishers, Chur, Switzerland, pp. 257–270.

Visalberghi, E. and Addessi, E. (2000), Response to changes in food palatability in tufted capuchin monkeys, *Cebus apella. Animal Behaviour*, 59: 231–238.

von Frisch, K. (1938), Zur Psychologie des Fische-Schwarmes, *Naturwissenschaften*, 26, 601-606. In Griffin, A. S., 2004, Social learning about predators: A review and prospectus, *Learning and Behaviour,* 32: 131-140.

Vonhof, M. J., Whitehead, H. and Fenton, M. B. (2004), Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats, *Animal Behaviour,* 68: 507-521.

Wagner, R. H. and Danchin É. (2003), Conspecific copying: a general mechanism of social aggregation, *Animal Behaviour*, 65: 405-408.

Walsh, W.J. (1985), Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography, *Bulletin of Marine Science*, 36: 357–376.

Want, S. C. and P. L. Harris. (1998), Indices of program-level comprehension, *Behavioural and Brain Sciences,* 21: 706–707.

Ward, A. J. W. and Hart, P. J. B. (2003), The effects of kin and familiarity on interactions between fish, *Fish and Fisheries*, 4: 348–358.

Ward, A. J. W. and Hart, P. J. B. (2005), Foraging benefits of shoaling with familiars may be exploited by outsiders, *Animal Behaviour*, 69: 329–335.

Ward, A. J. W., Hart, P. J. B. and Krause, J. (2004*a*), Assessment and assortment: how fishes use local and global cues to choose which school to go to, *Proceedings of the Royal Society B,* 271: S328–S330.

Ward, A. J. W., Thomas, P., Hart, P. J. B. and Krause, J. (2004*b*), Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*), *Behavioral Ecology and Sociobiology,* 55: 561–568.

Ward, A. J. W., Hart, P. J. B. and Krause, J. (2004c), The effects of habitat and diet-based cues on association preferences in threespined sticklebacks, *Behavioral Ecology*, 15: 925-929.

Ward, A. J. W., Holbrook, R. I., Krause, J. and Hart, P. J. B. (2005), Social recognition in sticklebacks: the role of direct experience and habitat cues, *Behavioral Ecology and Sociobiology*, 57: 575-583.

Ward, A. J. W., Webster, M. M. and Hart, P. J. B. (2007), Social recognition in wild fish populations, *Proceedings of the Royal Society of London Series B*, 274: 1071-1077.

Ward, A. J. W., Webster, M. M., Magurran, A. E., Currie, S., and Krause, J. (2009), Species and population differences in social recognition between fishes: a role for ecology?, *Behavioural Ecology*, 20: 511-516.

Warner, R. R. (1988), Traditionality of mating-site preferences in a coral reef fish, *Nature,* 335: 719-721.

Warner, R. R. (1990), Male versus female influences on mating-site determination in a coral-reef fish, *Animal Behaviour,* 39: 540-548.

Watts, D. J. and Strogatz, S. (1998), Collective dynamics of 'small-world' networks, *Nature*, 393:440–442.

Weatherley, A. H. and Gill, H. S. (1987), *The biology of fish growth,* Academic Press, London.

Webster, M. M., Adams, L. and Laland, K. N. (2008a), Diet-specific chemical cues influence association preferences and prey patch use in a shoaling fish, *Animal Behaviour,* 76: 17-23.

Webster, M. M., Atton, N., Hoppitt, W. J. E. and Laland, K. N. (2013), Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals, *The American Naturalist,* 181: 235-244.

Webster, M. M., Goldsmith, J., Ward, A. J. W. and Hart, P. J. B. (2007), Habitat specific chemical cues influence association preferences and shoal cohesion in fish, *Behavioral Ecology and Sociobiology*, 62: 273-280.

Webster, M. M. and Hart, P. J. B. (2006a), Subhabitat selection by foraging threespined stickleback (*Gasterosteus aculeatus*): previous experience and social conformity, *Behavioral Ecology and Sociobiology,* 60: 77–86.

Webster, M. M. and Hart, P. J. B. (2006b), Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution, *Behavioural Ecology*, 17: 959–964.

Webster, M. M. and Hart, P. J. B. (2007), Prior association mediates kleptoparasitic prey competition in shoals of threespined stickleback, *Animal Behaviour*, 74: 253-258.

Webster, M. M. and Laland, K. N. (2008), Social learning strategies and predation risk: Minnows copy only when using private information would be costly, *Proceedings of the Royal Society B,* 275: 2869–2876.

Webster, M. M. and Laland, K. N. (2009), Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus, Journal of Fish Biology*, 75: 1868–1873.

Webster, M. M. and Laland, K. N. (2011), Reproductive state affects reliance on public information in sticklebacks, *Proceedings of the Royal Society B*, 278: 619-627.

Webster, M. M. and Laland, K. N. (2012), The learning mechanism underlying public information use in ninespined sticklebacks **(***Pungitius pungitius***),** *Journal of Comparative Psychology, Advance online publication.*

Webster, M. M., Ward, A. J. W. and Hart, P. J. B. (2008b), Shoal and prey patch choice by co-occurring fish and prawns: inter-taxa use of socially transmitted cues, *Proceedings of the Royal Society of London Series B*, 275: 203-208.

West, J. E., Buckley, R. M. and Doty, D. C. (1994), Ecology and habitat use of juvenile rockfishes (*Sebastes* spp.) associated with artificial reefs in Puget Sound, Washington, *Bulletin of Marine Science*, 55: 344–350.

Wey, T., Blumstein, D. T., Shen, W. and Jordan, W. (2007), Social network analysis of animal behaviour: a promising tool for the study of sociality, *Animal Behaviour*, 75: 333–344.

Whitehead, H. (1997), Analysing animal social structure, *Animal Behaviour*, 53:1053–1067.

Whiten, A. (1998), Imitation of the sequential structure of actions by chimpanzees (*Pan trologdytes*), *Journal of Comparative Psychology*, 112: 270–281.

Whoriskey, F. G. and Fitzgerald, G. J. (1994) Ecology of the threespined stickleback on the breeding grounds. *In*, Bell, M. A. and Foster, S. A. *eds.*, *The Evolutionary Biology of the Threespined Stickleback*, p. 438–471. Oxford University Press, Oxford, New York, Tokyo.

Wilkinson, G. (1992), Information transfer at evening bat colonies, *Animal Behaviour,* 44: 501–518.

Wisenden, B. D., Chivers, D. P. and Smith, R. J. F. (1995), Early warning of risk in the predation sequence: a disturbance pheromone in Iowa darters (*Etheostoma exile*), *Journal of Chemical Ecology*, 21: 1469- 1480.

Witte, D. J. and Ryan, M. J. (1998), Male body length influences female mate-choice copying in the sailfin molly (*Poecilia latipinna*), *Behavioural Ecology,* 9: 534-539.

Witte, D. J. and Ryan, M. J. (2002), Mate-choice copying in the sailfin molly, *Poecilia latipinna*, in the wild, *Animal Behaviour,* 63: 943-949.

Wolf, J. B. W., Mawdsley, D., Trillmich, F. and James, R. (2007), Social structure in a colonial mammal: Unravelling hidden structural layers and their foundations by network analysis, *Animal Behaviour*, 74: 1293-1303.

Wootton, R. J. (1976), The biology of the sticklebacks. Academic Press, New York.

Wootton, R. J. (1994), Energy allocation in the threespined stickleback. In The evolutionary biology of the threespined stickleback (ed. M. A. Bell & S. A. Foster), pp. 116-143. Oxford: Science Publications.

Zentall, T. R. (1996), 'An analysis of imitative learning in animals.' In *Social Learning in Animals: The Roots of Culture*, edited by C. M. Heyes and B. G Galef, Jr., 221–234. London: Academic Press.

Zentall, T. and Galef, B. G. Jr. (1988), *Social Learning: Psychological and Biological Perspectives*, Lawrence Erlbaum Associates, Hillsdale.

Zentall, T. R., Sutton, J. E. and Sherburne, L. M. (1996), True imitative learning in pigeons, *Psychological Science*, 7: 343–346.